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THE UNIVERSITY OF ALBERTA
ASPECTS OF THE COMMUNITY ECOLOGY OF CORAL REEF FISHES AT
CURACAO, NETHERLANDS ANTILLES

by



BRIAN E. LUCKHURST

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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DEPARTMENT ZOOLOGY

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THE UNIVERSITY OF ALBERTA
FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and
recommend to the Faculty of Graduate Studies and Research,
for acceptance, a thesis entitled Aspects of the community
ecology of coral reef fishes at Curaçao, Netherlands Antilles
submitted by Brian E. Luckhurst
in partial fulfilment of the requirements for the degree of
Doctor of Philosophy.

ABSTRACT

The resident fish communities in four quadrats (10m, 20m, 30m, 40m depth) along three transects on the fringing reef of Curaçao, and one transect at Bonaire, were basically similar in trophic composition, activity periods and home range designations. The dominant trophic group was the planktivores. Most of the resident fishes were diurnally active and the cryptic element of the communities was substantial. At night, non-resident planktivores sheltering in the quadrats were very abundant; the numbers of apogonids were considerably greater than during the day.

Similarity in species composition as measured by the coefficient of community (CC) and Euclidean distance (D) showed the greatest change between 10m and 20m. The CC values for the deeper communities (30m and 40m) exhibited high similarity, but the D values were more variable. Communities from a number of quadrats at different depths demonstrated high similarity (D index). There was no systematic tendency for communities at the same depth to have similar D values.

There were few changes in the species composition of the communities over the 18 month study period. Several cases of the possible "extinction" of a species were found.

The diversity patterns (Hill's numbers) along the transects showed that species richness (N_0) declined from 20m to 40m. The two diversity measures, N_1 and N_2 , exhibited no consistent trends along any of the transects. The beta diversity of the transects ranged from 0.57 at Bonaire to a maximum of 1.00 at Curaçao.

The recruitment patterns of 16 resident species from seven families were examined. Size-designated postlarval recruits were counted in all quadrats and the overall pattern of occurrence and abundance for the three Curaçao transects was determined. Most of the species had two peaks in abundance, one in the spring (March-May) and one in the autumn (September-November). The species with the largest sample sizes had recruits present essentially throughout the year.

A temporal analysis of four community parameters was made to detect evidence of changes in community structure and possible seasonal trends. Species richness was mainly linear with some fluctuations. The number of fishes (NCP) exhibited large fluctuations in abundance which appeared to be seasonal. NCP was highly correlated with water temperature. The temporal variation in both diversity (N_1) and evenness ($E_{2.1}$) provided little evidence of seasonal changes.

A detailed analysis was made of the use of space by 25 resident species. The territorial pomacentrids had a strong influence on the use of space by other species. Within the reef infrastructure, the holocentrids showed the highest degree of spatial constancy. Many cases of the diurnal-nocturnal sharing of the same shelter site by different species were found.

The substrate rugosity (SR) patterns down the transects reflected a basic similarity in geomorphology between 20m and 40m. Vertical relief was correlated with the SR of each quadrat. A correlation was found between the resident species richness of a quadrat and its SR value. This relationship was tested in two experimental quadrats and the results were in agreement with those predicted.

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INTRODUCTION

Scleractinian coral reefs have a geological record which dates from the middle Triassic (Newell 1971). This long evolutionary development has culminated in modern coral-algal reefs of extraordinary biological complexity and high species richness in many taxa. The fishes associated with reefs show a bewildering array of shapes, colours and sizes, presumably the result of long-term speciation in a favourable, relatively constant environment. Smith and Tyler (1972) have postulated the major steps that may have occurred in the community evolution of reef fishes to their present day organization. A thorough review of the work on reef fishes (Ehrlich 1975) emphasizes the tremendous diversity in the behaviour and ecology of reef species as well as the coevolved nature of many relationships.

Much of the early work on reef fishes was essentially descriptive - faunal lists with natural history observations. The works of Beebe and Tee-Van (1933) and particularly Longley and Hildebrand (1941) are excellent examples of the pioneering studies in the field. Few of the other studies which followed dealt with reef fish communities although the study of Odum and Odum (1955) of the organic productivity of an atoll included a trophic and biomass assessment of the fish fauna. Bardach (1959) estimated the summer standing crop of reef fishes in Bermuda, as well as the extent of movement of some species (Bardach 1958). He found that several species showed a tendency to return to a home reef. Springer and McErlean (1962) obtained similar results with tagged fishes in Florida. An

important contribution to community ecology was the work of Hiatt and Strasburg (1960) who described the habitat and feeding relationships of a large number of species on a Pacific reef. A comparison of the standing crops of reef fishes of an artificial reef and a natural reef (Randall 1963) showed the potential of artificial reefs in increasing the standing crop in an area by providing suitable shelter. Clark et al. (1968) investigated a reef fish shore community in the Red Sea and obtained estimates of both species richness and biomass.

Talbot (1965) demonstrated the influence of different coral substrates on the fish species composition of a reef off East Africa. He showed that many species were restricted in their habitat distribution. Talbot and Goldman (1972) and Goldman and Talbot (1976) have shown that different habitat zones of a reef have distinctive fish faunas as well as a different trophic composition. In a detailed analysis of a single community, Smith and Tyler (1972) discussed the space sharing mechanisms which enhance species packing in coral reef fish communities. A subsequent work dealt with the succession and stability of fish communities on patch reefs (Smith and Tyler 1975). This was the first attempt to describe temporal changes in reef fish community structure and diversity as influenced by changes in the substrate. The importance of the individual size of infaunal species in regulating the occurrence and relative abundance of other species in the community has been postulated by Smith (1975).

The elucidation of the population structure of reef

fish communities is difficult, owing to the wealth of interacting factors. As coral reefs are only found in a benign, relatively predictable environment, the organisms living on them comprise biologically accommodated communities (Sanders 1968). Hence, interactions, mainly competition and predation, will be the principal forces shaping the communities. Symbiotic relationships, particularly those involving commensal "cleaners", are also well developed in reef fishes (Losey 1972). The influence of one species of "cleaner" fish on the point diversity of reef fishes has been demonstrated by Slobodkin and Fishelson (1974).

The high degree of species packing suggests that competition is probably an important factor influencing community structure in reef fishes. Connell (1975) has suggested that in areas with benign physical conditions, such as coral reefs, predation is more intense than in areas with severe physical conditions, and that many species seldom reach population densities where competition is likely to occur. This leads to the possibility that predation may be more important in determining the community structure of reef fishes than competition. However, little is known of the ecology and population dynamics of most coral reef predators (with the exception of a few commercially important species). Thus, evaluation of the influence of predators on community structure will have to await more knowledge of their species biology. Assuming that predation is very intense on reefs, then suitable refuges for prey species will be extremely important in determining community composition. Smith and Tyler (1972) have emphasized the cri-

tical nature of adequate refuges for reef fishes. Competition for a limited number of such refuges will undoubtedly occur, but whether it will be more important than predation in shaping community structure is not known.

The nature of competition between reef fishes is blurred by the fact that many species are habitat and food generalists. There is considerable overlap in both habitat (e.g. Bradbury and Goeden 1974) and diet (e.g. Emery 1973) in many coexisting species. Sale's (1974, 1975) studies of guilds of territorial pomacentrids has considerably clarified the nature of the interactions between, and the coexistence of, the guild members. He has shown that chance mortality and recruitment play a very significant role in determining small scale species composition.

As predation occurs unpredictably in time and space, vacated areas may appear at any time on the reef. The availability of recruits to colonize such areas will be dependent on the spawning periodicity of the populations in the region. The presence of a permanent pool of recruits ready to utilize vacated space would be beneficial for a species. The patterns of reproductive periodicity may therefore have evolved to maintain a continual source of recruits as potential colonizers and to buffer predation losses.

There are few studies dealing with reproductive seasonality in reef fishes in the Caribbean. Erdman (1956) presents evidence of periodicity in spawning of fishes in Puerto Rico. The occurrence of ripe fishes or the presence of very young

individuals was considered as evidence of spawning activity. Munro et al. (1973) provide records of the time of spawning of 83 species of reef fishes in Jamaica. Details of seasonality in spawning are given for 35 species. These authors determined that there was a general spawning peak from February to April, although some families showed evidence of spawning throughout the year. Powles (1975) studying larval fishes around Barbados found that there were two peaks of abundance in most of the in-shore reef fish families, a spring peak (March to May) and an autumn peak (August to October). Corresponding recruitment peaks would be expected to occur following these peaks in larval abundance.

Most of the studies dealing with recruitment in reef fishes have centred on experimental rather than natural habitats. In these studies, recruits were any fishes, juvenile or mature, which were attracted to the experimental structures. Sale and Dybdahl (1975) have shown that recruitment to a series of small experimental habitats (live coral and coralline rock) on the Great Barrier Reef shows a seasonal periodicity, but does occur throughout the year. There was evidence for a restricted recruitment period in only three species out of the 56 studied. Russel et al. (1974) have shown that recruitment to a series of artificial reefs in the same area is markedly seasonal and is mainly by juveniles.

Most studies of reef fish communities have been of short duration providing only a brief glimpse of long term processes such as recruitment, and changes in species richness,

diversity or numbers of fishes. Other studies have sampled the same communities at variable time intervals and examined the differences between samples for evidence of changes in the community (Smith 1973; Smith and Tyler 1975). The similarity of samples collected repeatedly from the same experimental habitats has been used to test theories of reef fish community structure (Sale and Dybdahl 1975). Continuous monitoring with short time intervals between samples is the most effective means of determining the constancy or degree of change of parameters over an annual cycle. Such studies in reef areas are few in number. One of the purposes of this study was to provide insight into the natural fluctuations of community parameters over an extended period.

The significance of space as a limiting resource in reef fish communities (Smith and Tyler 1972) and in guilds of pomacentrids (Sale 1975) has recently been investigated. Sale (1975) has shown that the total amount of space used by guild members on three different rubble patches did not change significantly over a one year period. The constant use of space by territorial pomacentrids is well documented (Low 1971; Rasa 1969; Myrberg and Thresher 1974). However, little is known about the use of space by the smaller, less conspicuous members of the reef community, particularly those residing within the reef infrastructure. Information is presented here which provides insight into the use of space by the cryptic members of the community as well as furthering previous findings on pomacentrids.

Owing to the dependence of most reef fishes on the substrate for shelter, as well as food, it may be expected that the nature of the substrate will strongly influence the species composition and diversity of fishes in an area. The effect of spatial heterogeneity on community diversity was first investigated by terrestrial ecologists. They have devised various measures of habitat complexity and have attempted to correlate them with species richness or diversity. Most of these measures quantify the heterogeneity or patchiness of the habitat under study. Significant correlations have been found in a wide range of taxa including rodents (Rozenzweig and Winakur 1969; M'Closkey 1976), birds (MacArthur et al. 1962; MacArthur 1964; Roth 1976), lizards (Pianka 1966) and insects (Murdoch et al. 1972).

Few studies have attempted to quantify substrate complexity in marine or aquatic habitats. Kohn (1967) and Kohn and Leviten (1976) found a positive correlation between measures of habitat complexity and species richness in tropical gastropod molluscs. Harman (1972) found a similar correlation between substrate diversity and mollusc species diversity in lakes. The diversity of tidepool fishes has been shown to be correlated with habitat diversity (Weaver 1969).

Only two studies have provided estimates of the substrate complexity of an area on the reef and sought correlations of this measure with the fish species richness or diversity found there (Risk 1972; Talbot and Goldman 1972). Both studies obtained positive correlations between these variables using

different substrate measures. I have used three different substrate variables, including a measure of substrate rugosity, in correlations with various community parameters, to determine what relationships might exist between them.

In this study, I have examined several different aspects of reef fish communities. I start by analyzing the diurnal species composition and structure of the communities along a depth gradient. The nocturnal communities of these same quadrats are briefly discussed and major differences between the diurnal and nocturnal communities are noted. An analysis of the numerical aspects of the communities follows. The periodicity and abundance of the recruits of 16 species commonly found in the quadrats are figured. The temporal variation in the community parameters of each quadrat is examined to detect seasonal changes.

A detailed examination is made of the use of different kinds of shelter sites in the quadrats by 25 of the resident species. I believe this is the first record of long term observations of the use of space by reef fish species. The sharing of the same shelter site in "shifts" by different species is demonstrated. Finally, I look at the substrate variables along the transects and investigate the correlations between them and various parameters of the communities and of selected species.

LOCALITY

The Leeward group of the Netherlands Antilles - Aruba, Curaçao and Bonaire - form an island chain parallel to the Venezuelan coast. Curaçao ($12^{\circ}2'-12^{\circ}23'N$; $68^{\circ}44'-69^{\circ}10'W$) lies about 70 km off the coast and Bonaire is approximately 50 km due east. These two islands were the sites for the study.

Conditions for coral reef development are nearly ideal around the two study islands. The surface water temperature varies annually from about 25° to $28^{\circ}C$. The mean annual variation at 45m depth is $2.0^{\circ}C$ (Wüst 1964). Temperatures taken with a hand-held thermometer in situ, throughout the course of the study, did not differ significantly from this range (Fig. 1). On several occasions, a thermocline moved up the reef slope to a depth of 30 m. This usually occurred in February-April, the period of minimum water temperatures. The lowest temperature recorded below the thermocline was $24.3^{\circ}C$. The maximum difference measured across the thermocline was $1.4^{\circ}C$.

The surface salinity remains nearly constant at 35.8 ‰, with a mean annual variation of 0.20 ‰ (Wüst 1964). The tidal range is small and amounts to about 30 cm daily. The maximum range is 55 cm. The trade winds blow almost continuously from an easterly direction at a mean velocity of 6.7 m/sec. The currents along the southwest (SW) coast of Curaçao generally flow in a northwesterly direction. The flow exceeds 1 knot (1.85 km/h), only 6% of the time, near the entrance to Willemstad harbour (Meyer 1973). However,

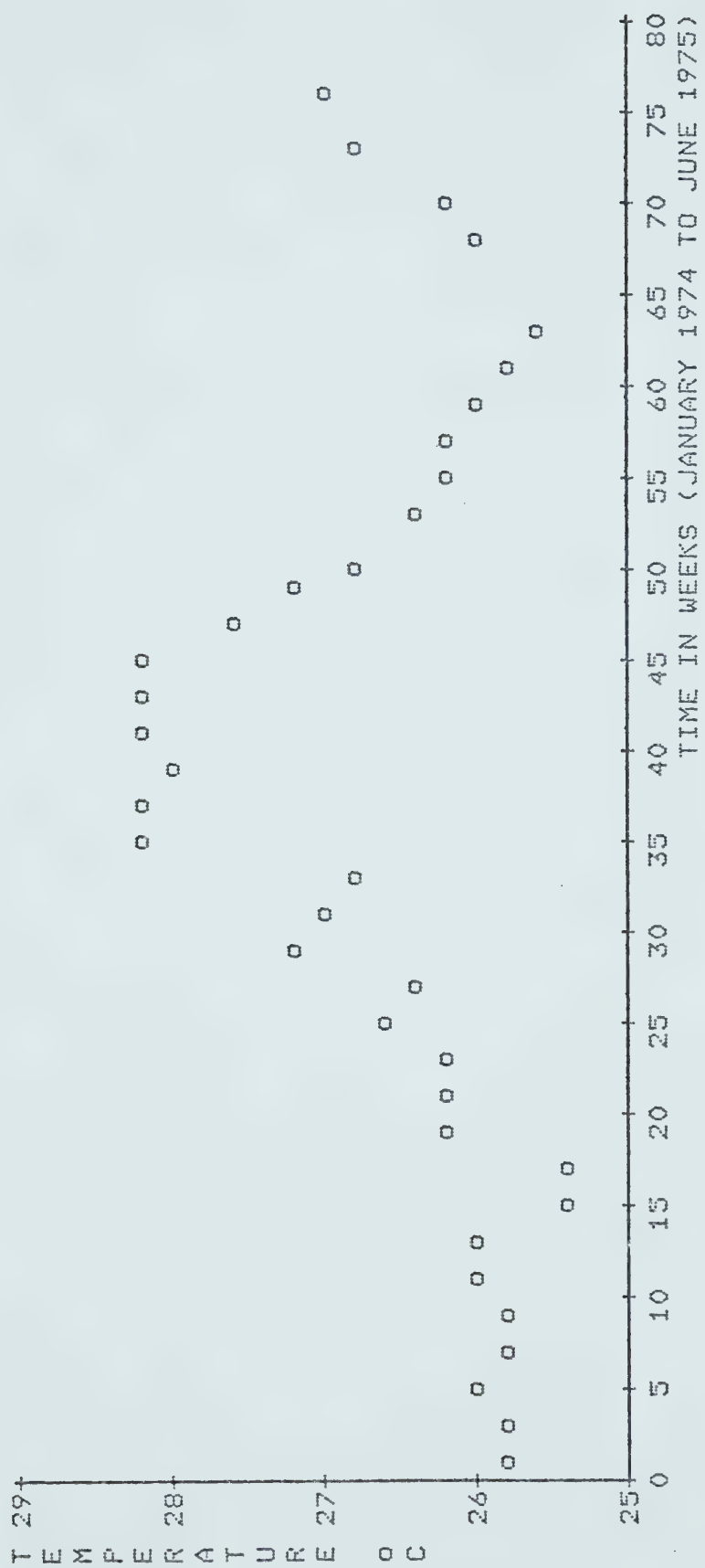


FIG. 1 - Water temperature at 10 m depth at Curaçao.

there is some local variation in this pattern and reversals of direction at different times and depths were observed.

The climate of both islands is semi-arid. Rainfall averages 50-55 cm/yr and usually occurs as short, heavy showers. Most precipitation falls during the period June to November (Wüst 1964). There is little runoff around the coasts of either island. The air temperature varies only slightly from a mean of 27.5°C.

The eastern (windward) coasts of both islands are subjected to heavy wave action, but prolific coral growth may occur in deeper, calmer water. The relatively calm, leeward coasts have well-developed fringing reefs. The reefs on the leeward (SW) coast of Curaçao are characterized by a narrow (25-100 m wide) terrace sloping seaward from a cliff or shingle beach to a drop-off at a depth of 7 to 12 meters. The angle of the seaward slope below the drop-off varies from 45° to almost vertical and this slope is covered by a rich coral growth. Roos (1964, 1971) and Bak (1975) have described the coral zonation and the ecological factors affecting coral growth around the coasts of both Curaçao and Bonaire.

The study area in Curaçao was a small section (400 m) of the SW coast near the entrance to Piscaderabaai (Fig. 2). The single site at Bonaire was on the west coast at Karpata (Fig. 3). Van den Hoek et al. (1975) have described the zonation of algae, corals and gorgonians along a transect at the Curaçao site; Scatterday (1974) has discussed the coral assemblages and zonation found at Karpata.

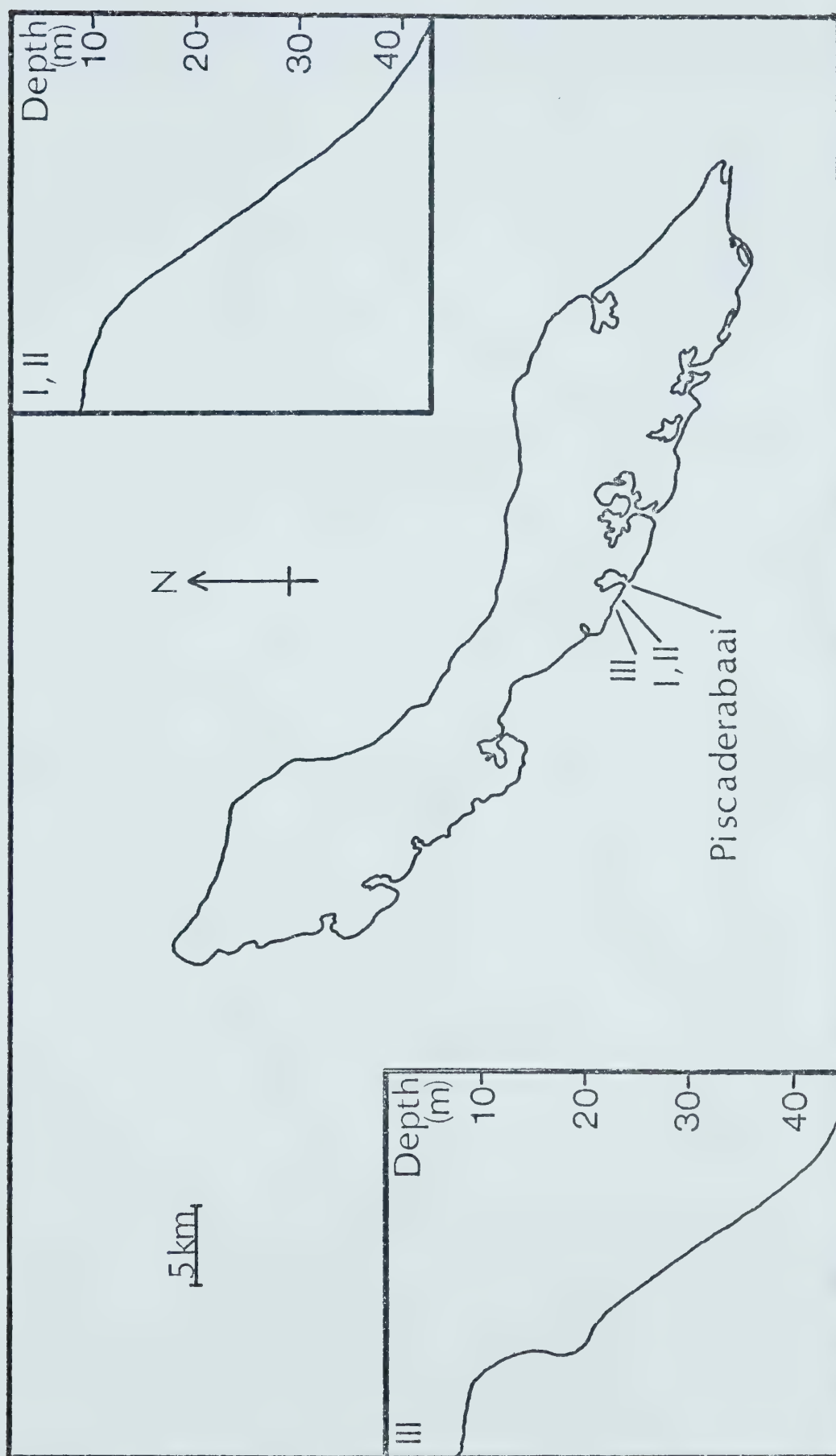


FIG. 2 - Map of Curaçao, Netherlands Antilles, indicating the location of the study sites near Piscaderabaai. The insets are the reef profiles of the transects (I, II, III).

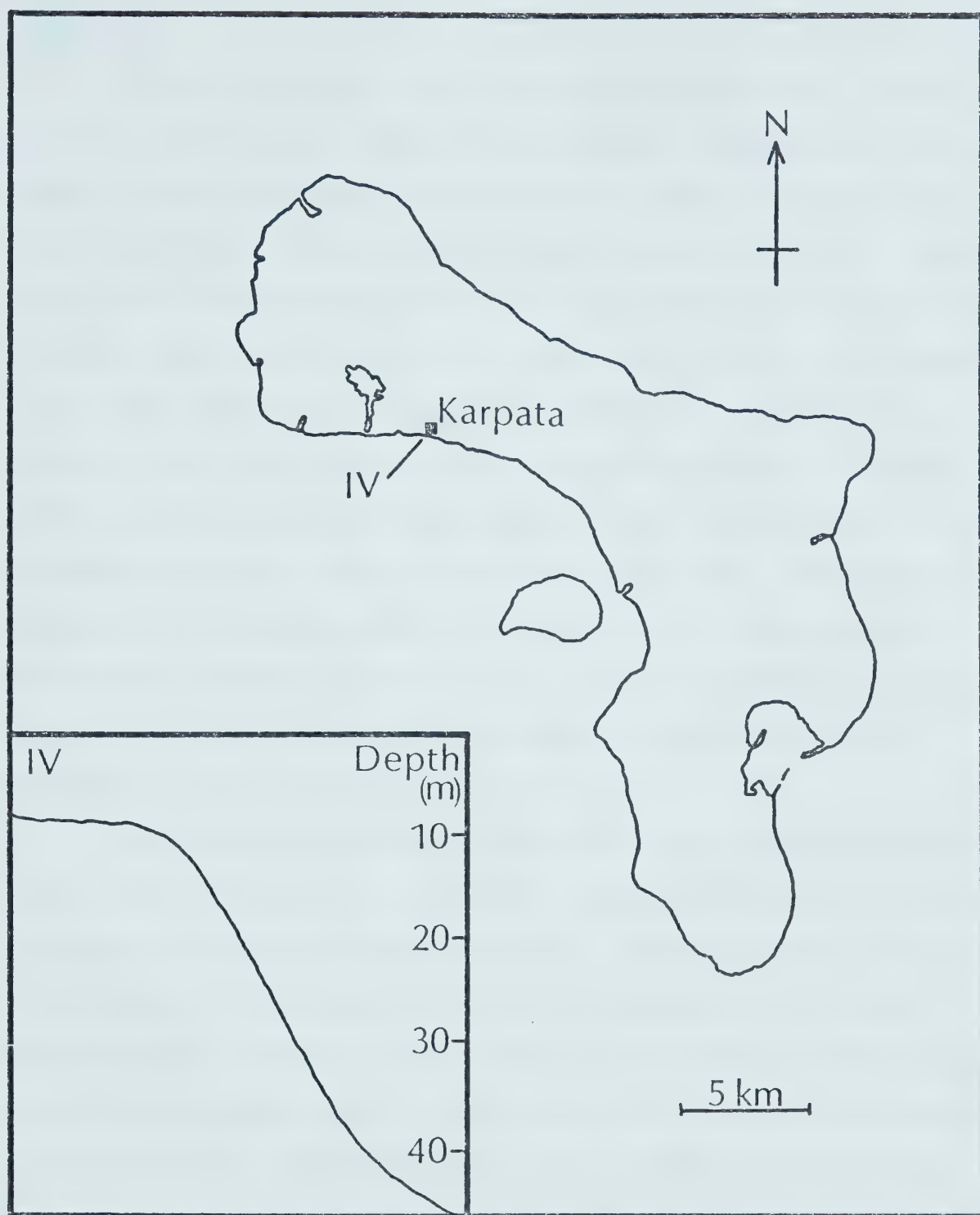


FIG. 3 - Map of Bonaire, Netherlands Antilles, indicating the location of the study site at Karpata. The inset is the reef profile of the transect (IV).

METHODS

Three transects were established in Curaçao. Transects I and II were within 25 m of each other, while transect III was about 400 m further west along the coast (Fig. 2). There was only a single transect at Bonaire (Fig. 3). Quadrats ($3\text{ m})^2$ were roped off with 6.3 mm ($\frac{1}{4}$ ") nylon line along the transects at depths of 10m, 20m, 30m and 40m. The quadrats along transects I and II were first photographed in December 1973 and transect III was photographed in January 1974. Another series of photographs was taken of all of the Curaçao quadrats in August 1974 and June 1975. The Bonaire quadrats were photographed in September 1974 and May 1975. The series of photographs of each quadrat enabled me to assess changes in the substrate which might be correlated with changes in fish community composition.

All photographs were taken with high speed black and white film (Kodak Tri-X, ASA 400), using a Nikonos II camera fitted with a 15 mm lens (fish-eye). Prints (20 cm x 25 cm) were made of each quadrat and outline copies of the main features were drawn on waterproof paper. These outline maps were subsequently used to plot the shelter sites, home ranges and territories of the various species during each census.

In Curaçao, a visual census was made of the fish present in each quadrat approximately every two weeks over the period January 1974 to June 1975. The Bonaire site was visited in June and September 1974 and February and May 1975. All observations were made using SCUBA. Census dives were

conducted at either 0900 hours or 1430 hours. A total of over 580 hours was spent underwater in data collection. The species generally considered as resident in a community (Smith and Tyler 1972, 1975) were emphasized, thus, territorial species and those with small home ranges tend to predominate. Particular emphasis was placed on determining the presence and abundance of the cryptic members of the community. Specific shelter sites were often marked with a small stainless steel pin, driven into the substrate, to facilitate monitoring. Wandering herbivores, such as acanthurids and scarids and the ubiquitous and free-ranging labrids were not included in the diurnal censuses. Labrids were, however, counted during nocturnal censuses as they constituted a significant proportion of the nocturnal community.

A series of nocturnal dives (between 2000-2200 hours) was conducted in Curaçao from October 1974 to March 1975. All quadrats were censused three times during this period by me and my diving partner, yielding a total of 36 sets of observations for the three transects. Many supplementary observations were made outside of the quadrats.

All species were divided into three size classes: post-larval (recruit), juvenile and mature. The size limits were established from information from the literature and by assessment of sizes in the field. Collections of specimens were made to confirm species identification and size estimates.

During each census, all of the fishes in a quadrat

were counted by me and my diving partner. Results were recorded on roughened plastic (Perspex) sheets with a pencil. The technique was as follows: starting three to four meters above the substrate and to either side of the quadrat, all identifiable species, at that distance, were counted. Next, after moving down to about one meter above the substrate, the smaller species were counted. Finally, the quadrat was divided into halves and the small, cryptic species in each half were censused separately by both observers. The presence of these individuals was detected by systematically moving a hand over sand patches and corals, and by shining powerful diving lights into all caves and crevices. It appeared that the presence of most individuals was detected before they reacted to the light. Poisoning of quadrats to obtain estimates of abundance was precluded owing to the long term nature of the study.

The nocturnal technique was essentially the same except that the diving lights were constantly on and a third diver was present to act as a "lookout". It was difficult to identify and count some of the species feeding high in the water column above the quadrats; as a consequence, the species remaining close to the substrate were emphasized. Some species were undoubtedly disturbed by the lights but I believe their presence was usually detected before they moved away.

The counts made by each observer were compared after each census. Time limitations at the greater depths did not

permit comparisons in situ. As a result, mean values were entered for a species when there was a discrepancy. The abundance of small species forming aggregations, e.g. the goby, Coryphopterus personatus (Jordan and Thompson) was estimated to the nearest five fish. These estimates and those of the sand dwelling gobies, C. glaucofraenum Gill and Gnatholepis thompsoni Jordan were more subject to error than the counts of other species.

In order to get an indication of whether the limited time at the greater depths had an influence on data collection, a comparison (F_{\max} test) was made of the variances of the number of species observed per census at the four depths throughout the study. Results from transect II did not show significant variance ($F_{\max} = 1.38$), while transects I ($F_{\max} = 4.30$, $p < 0.05$) and III ($F_{\max} = 2.99$, $p < 0.05$) did show significant variances. However, the variances at the latter two transects were greatest at 10 and 20 m respectively, while the lowest values at both transects were at 40 m. Such results suggest that the differences in the time spent at censusing do not affect the comparability of the data from different depths.

Several physical parameters were determined for the substrate of each quadrat. These included a measure of surface rugosity, vertical relief, coral species richness and percent coverage by ramose and glomerate corals. An estimate of the surface rugosity in each quadrat was obtained by the following technique: each quadrat was divided into rectangles

by positioning clothes pins at 50 cm intervals around the rope border of the quadrat and attaching a rope between pairs of pins on opposite sides. A fine link brass chain (1 link = 1.5 cm) was laid over the substrate directly under the rope and was made to conform as closely as possible to all contours and crevices. A measure of the actual surface distance relative to linear distance is obtained. This ratio is termed the substrate rugosity (SR) index. The procedure is repeated every 50 cm for the dimension parallel to the drop-off and then perpendicular to it. Measurements were made in both dimensions because some coral species have a tendency to grow horizontally outward from a steep slope and thus form wide ledges. It was felt that these ledges might significantly increase the amount of shelter. In addition, the vertical relief (VR), measured as a perpendicular from the lowest point on the substrate, was recorded at each 50 cm interval along the rope. Thus, a total of fourteen SR measurements and 49 VR measurements were obtained for each quadrat. If this technique were to be used when dealing with quadrats of a different size, the interval and number of measurements could be adjusted to the required degree of accuracy. The mean value of the SR and VR measurements was calculated for each quadrat and these values were used in later analyses. Coral species richness (CS) was determined by counting the number of species with live colonies approximately four cm or more in diameter.

The percentage cover by corals and sand in each quadrat was determined using photographs. Inherent in this method

is the error involved in estimating the area of three-dimensional structures from a two-dimensional photograph. Following Hiatt and Strasburg (1960), the corals were divided into two broad categories, glomerate and ramose. They were further subdivided into live and dead coral. Glomerate corals were all those species having a growth form which did not provide interstices for fishes. The coral rock substrate was included in this category despite the fact that some erosional features provided shelter. Ramose corals included all those species whose growth forms provided shelter, either horizontal or vertical, for fishes. The area of each category was determined with a compensating polar planimeter.

ANALYSIS OF FISH COMMUNITIES

Diurnal communities

The majority of the species considered in this study were chosen because they had territories or home ranges equal to, or smaller than, the size of the quadrat (9 m^2). They were also usually closely associated with the substrate i.e. benthic or epi-benthic. These are two distinct advantages for divers conducting detailed visual censuses.

The frequency and ease with which a given species can be observed in the field depends on many factors, but three are of general importance. Firstly, various aspects of the species biology - activity patterns, habitat, behaviour and feeding habits - must be considered. Territorial pomacentrids are conspicuous and can virtually always be counted when their territories are known, while small cryptic or nocturnal species may be observed infrequently because of their secretive habits. Secondly, the size of the territory or home range in relation to the size of the study area is important. The frequency with which a species should be observed is theoretically inversely proportional to the size of its home range. This problem was alleviated in this study owing to the concentration on non-labile species. Thirdly, the relative abundance of a species will influence the probability of detecting its presence. Rare species appear only occasionally in census data, while common species are almost always present.

The 65 species included in the study (Table 1) are listed in conventional phylogenetic order (American Fisheries

TABLE 1 - List of the 65 species included in the study in family order. All species are resident unless otherwise specified. Designations of trophic category (T), activity period (A) and home range (R) are given. The following abbreviations are used: for T, h-herbivore, o-omnivore, c-carnivore, v-piscivore, p-planktivore, e-ectoparasite cleaner, u-unknown; for A, d-diurnal, n-nocturnal, b-both; for R, rc-home range $<9m^2$ (conspicuous), rp-home range $<9m^2$ (cryptic), r+-home range $>9m^2$, s-sponge dweller.

	<u>T</u>	<u>A</u>	<u>R</u>
Muraenidae			
<u>Enchelycore nigricans</u> (Bonnaterre) ¹	c	n	r+
<u>Gymnothorax moringa</u> (Cuvier) ¹	v	n	r+
<u>Muraena miliaris</u> (Kaup) ¹	c	n	r+
Holocentridae			
<u>Holocentrus marianus</u> (Cuvier)	c	n	r+
<u>H. rufus</u> (Walbaum)	c	n	r+
<u>Myripristis jacobus</u> Cuvier	p	n	r+
<u>Plectrypops retrospinis</u> (Guichenot)	c	n	r+
Syngnathidae			
<u>Micrognathus ensenedae</u> (Silvester)	c	d	rp
<u>M. vittatus</u> (Kaup)	c	d	rp
Serranidae			
<u>Cephalopholis fulva</u> (Linnaeus)	c	b	r+
<u>Hyponlectrus chlorurus</u> (Valenciennes)	c	d	r+
<u>H. puella</u> (Cuvier)	c	d	r+
<u>H. unicolor</u> (Walbaum)	c	d	r+

	<u>T</u>	<u>A</u>	<u>R</u>
<u>Liopropoma carmabi</u> (Randall)	c	d	rp
<u>L. mowbrayi</u> Woods and Kanazawa	c	b?	rp
<u>L. rubre</u> Poey	c	d	rp
<u>Mycteroperca tigris</u> (Valenciennes) ²	v	b	r+
<u>Paranthias furcifer</u> (Valenciennes) ³	p	d	r+
<u>Petrometopon cruentatum</u> (Lacépède)	c	b	r+
<u>Serranus tabacarius</u> (Cuvier) ¹	c	d	r+
<u>S. tigrinus</u> (Bloch)	c	d	r+
Grammistidae			
<u>Rypticus saponaceus</u> (Bloch and Schneider) ¹	c	b	r+
<u>R. subbifrenatus</u> (Gill)	c	b	rp
Grammidae			
<u>Gramma loreto</u> Poey	p	d	rc
<u>Lipogramma trilineata</u> Randall	p	d	rp
Priacanthidae			
<u>Priacanthus cruentatus</u> (Lacépède)	p	n	r+
Apogonidae			
<u>Apogon lachneri</u> Böhlke	p	n	rp
<u>A. maculatus</u> (Poey)	p	n	rp
<u>A. phenax</u> Böhlke and Randall	p	n	rp
<u>A. planifrons</u> Longley and Hildebrand ²	p	n	rp
<u>A. townsendi</u> (Breder)	p	n	rp
<u>Phaeoptyx conklini</u> (Silvester)	p	n	rp
<u>P. xenus</u> (Böhlke and Randall)	p	n	rp
Pomadasyidae			
<u>Haemulon flavolineatum</u> (Desmarest)	c	n	r+

	<u>T</u>	<u>A</u>	<u>R</u>
Sciaenidae			
<u>Equetus punctatus</u> (Bloch and Schneider)	c	n	r+
Chaetodontidae			
<u>Centropyge argi</u> Woods and Kanazawa	h	d	rc
<u>Holacanthus tricolor</u> (Bloch)	c	d	r+
Pomacentridae			
<u>Chromis cyaneus</u> (Poey)	p	d	rc
<u>C. insolatus</u> (Cuvier)	p	d	rc
<u>C. multilineatus</u> (Guichenot) ³	p	d	r+
<u>C. scotti</u> Emery	p	d	rc
<u>Microspathodon chrysurus</u> (Cuvier)	h	d	r+
<u>Eupomacentrus dieneaeus</u> Jordan and Rutter	o	d	rc
<u>E. partitus</u> Poey	p	d	rc
<u>E. planifrons</u> Cuvier	o	d	rc
Cirrhitidae			
<u>Amblycirrhitus pinos</u> (Mowbray)	p	d	rc
Labridae			
<u>Bodianus rufus</u> (Linnaeus) juvenile ²	e	d	rc
<u>Clepticus parrai</u> (Bloch and Schneider) ³	p	d	r+
<u>Thalassoma bifasciatum</u> (Bloch) ³	c	d	rc
Clinidae			
<u>Acanthemblemaria spinosa</u> Metzelaar	p	d	rp
<u>Emblemaria bahamensis</u> (Stephens) ⁴	u	d	rp
<u>E. bottomei</u> (Stephens)	u	d	rp
<u>Starksia hassi</u> Klausewitz	c	d?	s
<u>Enneanectes atlorus</u> Rosenblatt	u	d	rp

	<u>T</u>	<u>A</u>	<u>R</u>
Blenniidae			
<u>Ophioblennius atlanticus</u> (Valenciennes) ²	h	d	rc
Gobiidae			
<u>Coryphopterus glaucofraenum</u> Gill	h	d	rc
<u>C. lipernes</u> Böhlke and Robins	p	d	rc
<u>C. personatus</u> (Jordan and Thompson)	p	d	rc
<u>Gnatholepis thompsoni</u> Jordan	h	d	rc
<u>Gobiosoma evelynae</u> Böhlke and Robins	e	d	rc
<u>G. horsti</u> Metzelaar	c	d	s
<u>G. randalli</u> Böhlke and Robins	e	d	rc
<u>Nes longus</u> (Nichols)	u	d	rp
<u>Quisquilius hipoliti</u> (Metzelaar)	p	d	rp
Canthigasteridae			
<u>Canthigaster rostrata</u> (Bloch)	o	d	r+

¹ visitor

² observed only in Bonaire quadrats

³ considered only in nocturnal censuses

⁴ I have collected information which indicates that this species is probably the male of Emblemaria bottomei. However, as it is ecologically distinct and has not yet been formally synonymized, I have left it as a separate species.

Society 1970). Most of the species listed are resident. They largely conform to Smith and Tyler's (1975) definition of resident species - "those (species) that had a definite home (=shelter site) within the study reef or whose home range included the study reef so that the same individuals returned repeatedly to the reef." In most studies, the designation of a species as resident has been based on short term observations; here, I consider the occurrence of species in 18 months of census data.

The procedure for determining the resident species in each quadrat requires some explanation. The probability of occurrence of a species in the census data was assigned to one of three categories, following an assessment of the factors, just discussed, associated with visual censusing. The major distinction was between species with a home range smaller than the quadrat i.e. $< 9 \text{ m}^2$ (r) and those with a home range larger (r+). The r category was further subdivided into species which were conspicuous (c) and those which were cryptic (p). This distinction was based on the colouration, behaviour and microhabitat of each species. The probabilities assigned to the three categories were as follows: rc - 75%, rp - 25% and r+ - 35%. These percentages should be considered as minima, i.e. the species would be expected to be present at least that percentage of the time, if it were resident. This is based on the assumption of Smith (1973) that acceptable microhabitats are consistently occupied by species that are adapted to them, although the occurrence of a given species in a particular

census is mainly a matter of chance.

The number of occurrences (%) of each species in a quadrat was determined for the period of the study; this percentage was tested (Chi-square) against the assigned probability of occurrence for that species. If the value was significantly ($p < 0.05$) below that expected, the species was not included as a resident in that quadrat. This procedure arbitrarily excludes some species, but emphasizes the consistency of occurrence as the most important aspect of residency. The physical changes in the substrates of the quadrats were relatively minor during the study. It seems unlikely, therefore, that such changes caused the permanent disappearance of any species.

All of the census data were used in the calculation of the community parameters. The initial data reduction was accomplished using a program, written in Fortran, which calculated parameter values for each sample as well as a mean value for the quadrat. Subsequent statistical analysis was performed using various programs in the APL statistics workspaces (STP2, STAT1, PSTAT) at the University of Alberta. Additional programs in another APL library (CHER) were used to calculate different indices e.g. Euclidean distance.

The diversity of each community was examined using Hill's diversity numbers (Hill 1973). The following parameters were determined for each quadrat: species richness, Hill's N_0 , total number of fishes (N), total number minus the goby Coryphopterus personatus (NCP), two measures of diversity, Hill's $N_1 (=e^{H'})$ and $N_2 (=1/\sum p_i^2)$ and Hill's evenness, $E_{2,1} (=N_2/N_1)$. N_1 , a heterogeneity index, is most sensitive to changes in the importance of the rarer species in a sample, while N_2 , a dom-

inance index, is most strongly affected by the commonest species (Peet 1974). Mean values of these community parameters for each quadrat are given in Table 2.

The rationale for including the NCP category was to decrease the bias in N caused by the abundance of Coryphopterus personatus in some quadrats. The mean values of N ranged from 28 to 409 individuals (Table 2). With the numbers of C. personatus removed, the range is 24 to 159 individuals. This species was most abundant in Bonaire where it ranged up to a mean of 250 individuals per quadrat (Table 2).

A correlation matrix of the mean community parameters from Curaçao (Table 3), produced a number of significant correlations. Species richness (N_0) was correlated with N and with NCP. The latter two parameters were themselves correlated probably because of collinearity with N_0 . Not surprisingly, N_1 and N_2 were the most highly correlated parameters (Hill 1973). Evenness was negatively correlated with both N_0 and N, but positively correlated with N_2 (Table 3).

An analysis of the diversity patterns down each transect (Fig. 4) revealed one consistent trend. In Curaçao, N_0 was always highest at 20 m and declined with depth. In Bonaire, there was a steady decline from 10 to 40m. The two measures of diversity N_1 and N_2 were highly variable and consistent trends with depth were not apparent. I have shown that N_0 is correlated with one of the substrate variables (SR) in the quadrats (Table 35). I believe that this relationship is at least partially a causal one. Thus, the pattern of N_0

TABLE 2 - Community parameters for Curaçao (transects I, II, III) and Bonaire (transect IV).
 Values are means \pm SE; for Curaçao N=36, for Bonaire N=5.

Quadrat	N ₀	N	NCP	N ₁	N ₂	E _{2.1}
I-10	13.9 \pm 0.5	111.6 \pm 7.2	109.7 \pm 6.6	5.441 \pm 0.250	3.244 \pm 0.154	0.599 \pm 0.009
I-20	17.2 \pm 0.3	200.4 \pm 8.5	122.6 \pm 5.9	7.348 \pm 0.305	4.902 \pm 0.282	0.653 \pm 0.012
I-30	12.9 \pm 0.3	71.8 \pm 4.8	58.9 \pm 3.5	8.230 \pm 0.194	6.237 \pm 0.186	0.755 \pm 0.010
I-40	9.6 \pm 0.3	28.0 \pm 1.5	25.5 \pm 1.6	6.825 \pm 0.194	5.306 \pm 0.199	0.773 \pm 0.012
II-10	16.2 \pm 0.5	112.4 \pm 5.7	112.4 \pm 5.7	7.721 \pm 0.252	5.077 \pm 0.160	0.661 \pm 0.008
II-20	19.8 \pm 0.4	168.0 \pm 10.8	89.8 \pm 4.4	8.169 \pm 0.511	5.017 \pm 0.428	0.588 \pm 0.015
II-30	12.3 \pm 0.4	82.5 \pm 5.0	65.7 \pm 4.1	6.951 \pm 0.208	5.123 \pm 0.195	0.732 \pm 0.011
II-40	13.2 \pm 0.4	85.0 \pm 5.9	40.1 \pm 2.6	5.661 \pm 0.324	3.604 \pm 0.258	0.623 \pm 0.011
III-10	17.9 \pm 0.5	93.5 \pm 5.5	89.1 \pm 4.5	10.248 \pm 0.255	7.282 \pm 0.172	0.710 \pm 0.006
III-20	21.5 \pm 0.7	210.4 \pm 11.6	106.8 \pm 6.6	7.433 \pm 0.394	4.059 \pm 0.259	0.538 \pm 0.010
III-30	16.7 \pm 0.6	179.5 \pm 11.8	51.0 \pm 2.6	4.386 \pm 0.369	2.364 \pm 0.195	0.552 \pm 0.011
III-40	12.2 \pm 0.4	38.9 \pm 3.3	24.3 \pm 1.2	8.207 \pm 0.443	6.272 \pm 0.448	0.743 \pm 0.018
IV-10	23.4 \pm 1.7	408.8 \pm 45.5	158.8 \pm 18.4	5.498 \pm 0.676	2.682 \pm 0.311	0.489 \pm 0.007
IV-20	17.4 \pm 1.6	261.2 \pm 44.7	50.2 \pm 5.6	3.016 \pm 0.641	1.699 \pm 0.258	0.587 \pm 0.031
IV-30	15.2 \pm 1.6	186.8 \pm 35.3	38.6 \pm 4.1	3.174 \pm 0.695	1.774 \pm 0.275	0.583 \pm 0.031
IV-40	14.2 \pm 1.4	198.4 \pm 32.5	48.4 \pm 5.7	3.266 \pm 0.415	1.923 \pm 0.257	0.591 \pm 0.024

TABLE 3 - Correlation coefficient matrix of the mean fish community parameters from 12 quadrats at Curaçao.

	N_0	N	NCP	N_1	N_2	$E_{2.1}$
N_0	1					
N	0.860***	1				
NCP	0.683*	0.682*	1			
N_1	0.227	-0.184	0.176	1		
N_2	-0.136	-0.482	-0.093	0.928***	1	
$E_{2.1}$	-0.730**	-0.828***	-0.470	0.464	0.755**	1

* $p < 0.05$

** $p < 0.01$

*** $p < 0.001$

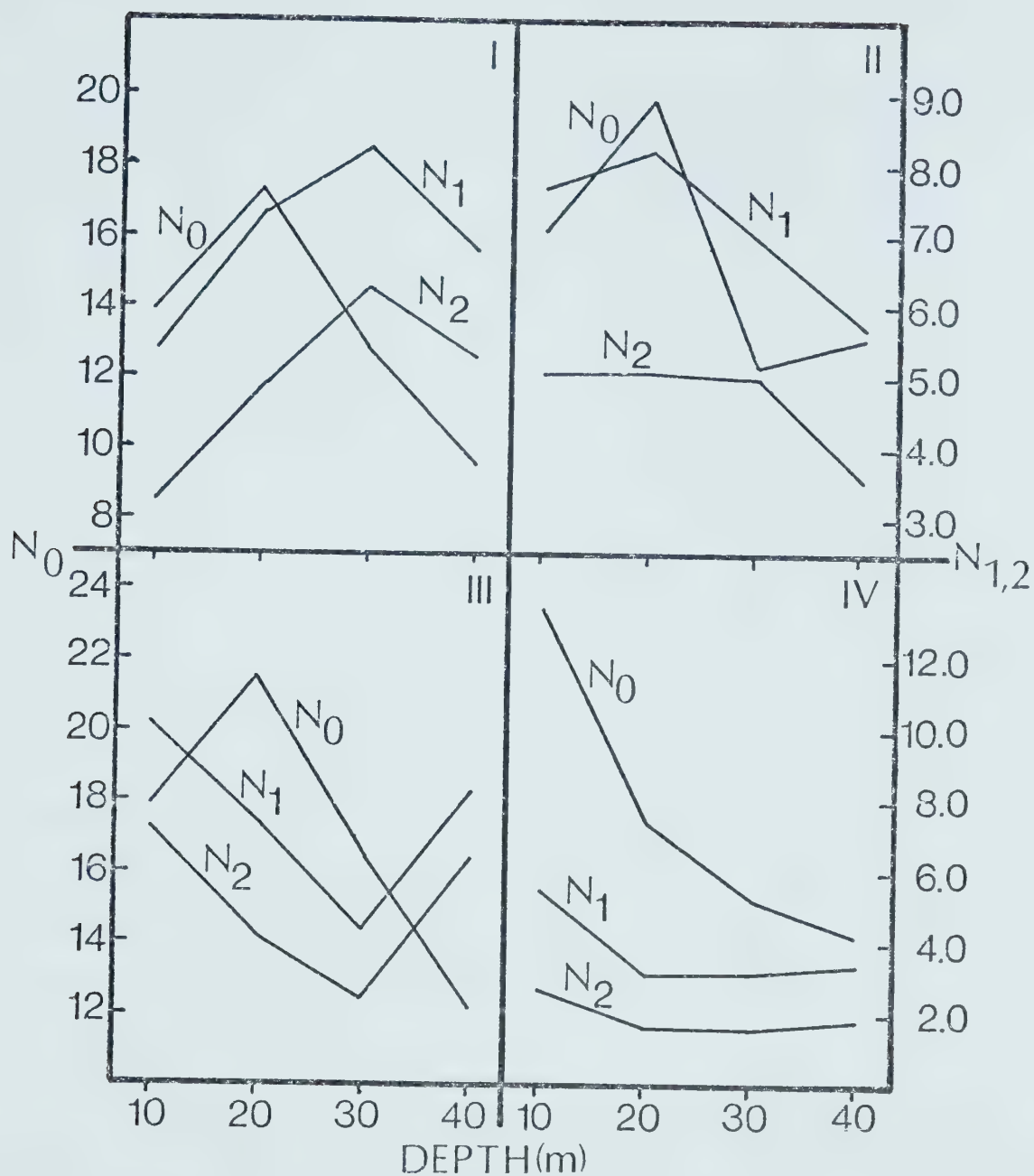


FIG. 4 - Diversity patterns along three transects (I, II, III) at Curaçao and one transect (IV) at Bonaire. The mean values of Hill's diversity numbers (N_0 , N_1 , N_2) are plotted.

along the transects cannot be attributed solely to a factor associated with depth.

The diversity of each transect (beta diversity) was calculated using the formula $BD = Sc/\bar{S}$ (Whittaker 1972), where Sc is the species richness of the composite sample (combining the four quadrats) and \bar{S} is the mean number of species per quadrat. The value of BD is an expression of the number of turnovers in species composition along the transect. Whittaker (1972) recommends using $(BD - 1)$ to express beta diversity, as a single sample may be considered to have zero beta differentiation. The beta diversity values of the four transects are given in Table 4. A value of zero indicates identical species composition and 1.0 a complete species turnover. Transect IV has just over half a species turnover, while transect I has a complete turnover. The two other transects have values intermediate to these. The differences in beta diversity between transects are further exemplified in the comparisons of species composition along the transects.

In order to compare the resident communities in each quadrat, two different indices were used. The Jaccard index, also known as a coefficient of community (CC) (Goodall 1973), considers only species presence or absence. It is calculated by the formula $CC = a/a+b+c$ where "a" is the number of species common to the two samples and "b" and "c" are the numbers of species exclusive to each of the two samples. The index ranges in value from zero (no species in common) to one (identical species composition).

TABLE 4 - Beta diversity (BD - 1) of three transects (I,II, III) at Curaçao and one transect (IV) at Bonaire.

Transect	BD - 1
I	1.00
II	0.81
III	0.74
IV	0.57

Euclidean distance, which may be used to measure community similarity (Heatwole and Levins 1972), takes into account the relative abundance of the species. It is calculated by the formula $D_{ij} = \left[\sum_{k=1}^s (p_{ik} - p_{jk})^2 \right]^{\frac{1}{2}}$ where "s" is the total number of species in the samples, p_{ik} is the proportion of individuals in community "i" that belong to the k^{th} species and p_{jk} is the equivalent proportion of individuals in community "j". Only the 42 most common species were used in the calculations. The values of D range from one (no similarity) to zero (identical samples).

All combinations of quadrats (120 pair-wise comparisons) were tested with each of the two indices (Table 5). A value of 0.750 for the CC index was chosen as the criterion for high similarity. The comparable value for the D index was 0.250. Only six pairs (5%) yielded CC values equal to or greater than the criterion. All of these pairs were quadrats at the same depth, and four of the six were at 40 m. This indicates a high degree of similarity in species composition in communities at this depth. In comparison, 29 pairs (24%) yielded D values equal to or less than 0.250, the D criterion. Six of the 29 pairs (21%) were quadrats at the same depth; 12 pairs (41%) were quadrats at adjacent depths and the remaining 11 pairs (38%) were not adjacent quadrats. In contrast to the CC index, three of the six pairs of quadrats showing high similarity at the same depth were at 20 m; only one pair was at 40 m.

Most of the pairs of quadrats with low D values were not at the same depth. This is evidence against the supposition that the presence and relative abundance of species is

TABLE 5 - Comparisons of resident fish communities at four depths (10m, 20m, 30m, 40m) along three transects (I, II, III) at Curaçao and one transect (IV) at Bonaire. The values of two indices are given - Euclidean distance above the diagonal and the coefficient of community below the diagonal. The series of underlined values are those down each transect (see Fig. 5).

	I				II				III				IV			
	10m	20m	30m	40m	10m	20m	30m	40m	10m	20m	30m	40m	10m	20m	30m	40m
I																
10m																
20m	<u>.367</u>	1	<u>.592</u>	<u>.623</u>	<u>.485</u>	<u>.725</u>	<u>.604</u>	<u>.777</u>	<u>.402</u>	<u>.713</u>	<u>.918</u>	<u>.710</u>	<u>.835</u>	<u>.979</u>	<u>.977</u>	<u>.946</u>
30m	<u>.286</u>	<u>.560</u>	1	<u>.159</u>	<u>.319</u>	<u>.365</u>	<u>.097</u>	<u>.385</u>	<u>.329</u>	<u>.371</u>	<u>.602</u>	<u>.323</u>	<u>.521</u>	<u>.685</u>	<u>.673</u>	<u>.634</u>
40m	<u>.250</u>	<u>.462</u>	<u>.571</u>	1	<u>.255</u>	<u>.484</u>	<u>.153</u>	<u>.490</u>	<u>.353</u>	<u>.489</u>	<u>.713</u>	<u>.416</u>	<u>.633</u>	<u>.795</u>	<u>.780</u>	<u>.738</u>
II																
10m	<u>.625</u>	<u>.355</u>	<u>.276</u>	<u>.241</u>	1	<u>.597</u>	<u>.301</u>	<u>.624</u>	<u>.281</u>	<u>.596</u>	<u>.828</u>	<u>.556</u>	<u>.744</u>	<u>.904</u>	<u>.892</u>	<u>.856</u>
20m	<u>.406</u>	<u>.655</u>	<u>.536</u>	<u>.448</u>	<u>.314</u>	1	<u>.367</u>	<u>.153</u>	<u>.518</u>	<u>.101</u>	<u>.283</u>	<u>.151</u>	<u>.196</u>	<u>.373</u>	<u>.360</u>	<u>.326</u>
30m	<u>.357</u>	<u>.708</u>	<u>.714</u>	<u>.522</u>	<u>.258</u>	<u>.731</u>	1	<u>.370</u>	<u>.350</u>	<u>.370</u>	<u>.590</u>	<u>.333</u>	<u>.512</u>	<u>.673</u>	<u>.658</u>	<u>.619</u>
40m	<u>.267</u>	<u>.519</u>	<u>.500</u>	<u>.842</u>	<u>.219</u>	<u>.552</u>	<u>.652</u>	1	<u>.567</u>	<u>.112</u>	<u>.226</u>	<u>.197</u>	<u>.169</u>	<u>.311</u>	<u>.294</u>	<u>.253</u>
III																
10m	<u>.607</u>	<u>.455</u>	<u>.387</u>	<u>.273</u>	<u>.586</u>	<u>.529</u>	<u>.406</u>	<u>.324</u>	1	<u>.518</u>	<u>.746</u>	<u>.478</u>	<u>.657</u>	<u>.821</u>	<u>.813</u>	<u>.777</u>
20m	<u>.424</u>	<u>.613</u>	<u>.552</u>	<u>.419</u>	<u>.333</u>	<u>.800</u>	<u>.679</u>	<u>.516</u>	<u>.543</u>	1	<u>.250</u>	<u>.173</u>	<u>.163</u>	<u>.332</u>	<u>.323</u>	<u>.288</u>
30m	<u>.281</u>	<u>.630</u>	<u>.696</u>	<u>.583</u>	<u>.235</u>	<u>.714</u>	<u>.783</u>	<u>.708</u>	<u>.371</u>	<u>.613</u>	1	<u>.360</u>	<u>.121</u>	<u>.100</u>	<u>.083</u>	<u>.064</u>
40m	<u>.207</u>	<u>.520</u>	<u>.571</u>	<u>.778</u>	<u>.200</u>	<u>.500</u>	<u>.591</u>	<u>.750</u>	<u>.273</u>	<u>.467</u>	<u>.583</u>	1	<u>.279</u>	<u>.447</u>	<u>.430</u>	<u>.390</u>
IV																
10m	<u>.417</u>	<u>.459</u>	<u>.400</u>	<u>.371</u>	<u>.368</u>	<u>.568</u>	<u>.500</u>	<u>.417</u>	<u>.415</u>	<u>.622</u>	<u>.459</u>	<u>.371</u>	1	<u>.203</u>	<u>.187</u>	<u>.152</u>
20m	<u>.314</u>	<u>.531</u>	<u>.571</u>	<u>.433</u>	<u>.306</u>	<u>.606</u>	<u>.586</u>	<u>.484</u>	<u>.359</u>	<u>.667</u>	<u>.581</u>	<u>.483</u>	<u>.639</u>	1	<u>.047</u>	<u>.082</u>
30m	<u>.257</u>	<u>.469</u>	<u>.556</u>	<u>.640</u>	<u>.250</u>	<u>.645</u>	<u>.571</u>	<u>.692</u>	<u>.378</u>	<u>.559</u>	<u>.679</u>	<u>.640</u>	<u>.462</u>	<u>.625</u>	1	<u>.052</u>
40m	<u>.235</u>	<u>.452</u>	<u>.538</u>	<u>.696</u>	<u>.229</u>	<u>.485</u>	<u>.556</u>	<u>.750</u>	<u>.256</u>	<u>.457</u>	<u>.667</u>	<u>.696</u>	<u>.447</u>	<u>.613</u>	<u>.714</u>	1

determined mainly by depth or some factor(s) associated with depth. About 15 resident species (25% of the total) were recorded at all depths and perhaps ten of these were found in every quadrat. Most of these species were gobiids. Goldman and Talbot (1976) found that only 7% of their total of 395 species were reef cosmopolitan (found in all habitats), while 11% were restricted to depths greater than 25 m, suggesting a true deeper reef fauna. In the present study, four resident species were normally found only at 30 or 40 m and may be considered deep reef species. However, as Colin (1974) has pointed out, some species have different bathymetric ranges in different localities. Differences in the depth range of several species were noted between Curaçao and Bonaire e.g. both Gramma loreto and Liopronoma rubre were common at 10 m in Bonaire but were never recorded in the Curaçao quadrats at that depth. These differences are probably attributable to local environmental variation, mainly in the substrate.

An examination of the index values down each transect (Table 5) shows that there is a clear trend for the CC index to decrease with increasing depth along all four transects. This relationship may be depicted as a graph of index values against depth (Fig. 5), where each of the deeper communities is compared to the 10 m community. The greatest change in CC occurs between 10 and 20 m. The communities at the greater depths show little change with respect to 10 m. The D values show a similar trend between 10 and 20 m, but the deeper communities are far more variable (Fig. 5). The large num-

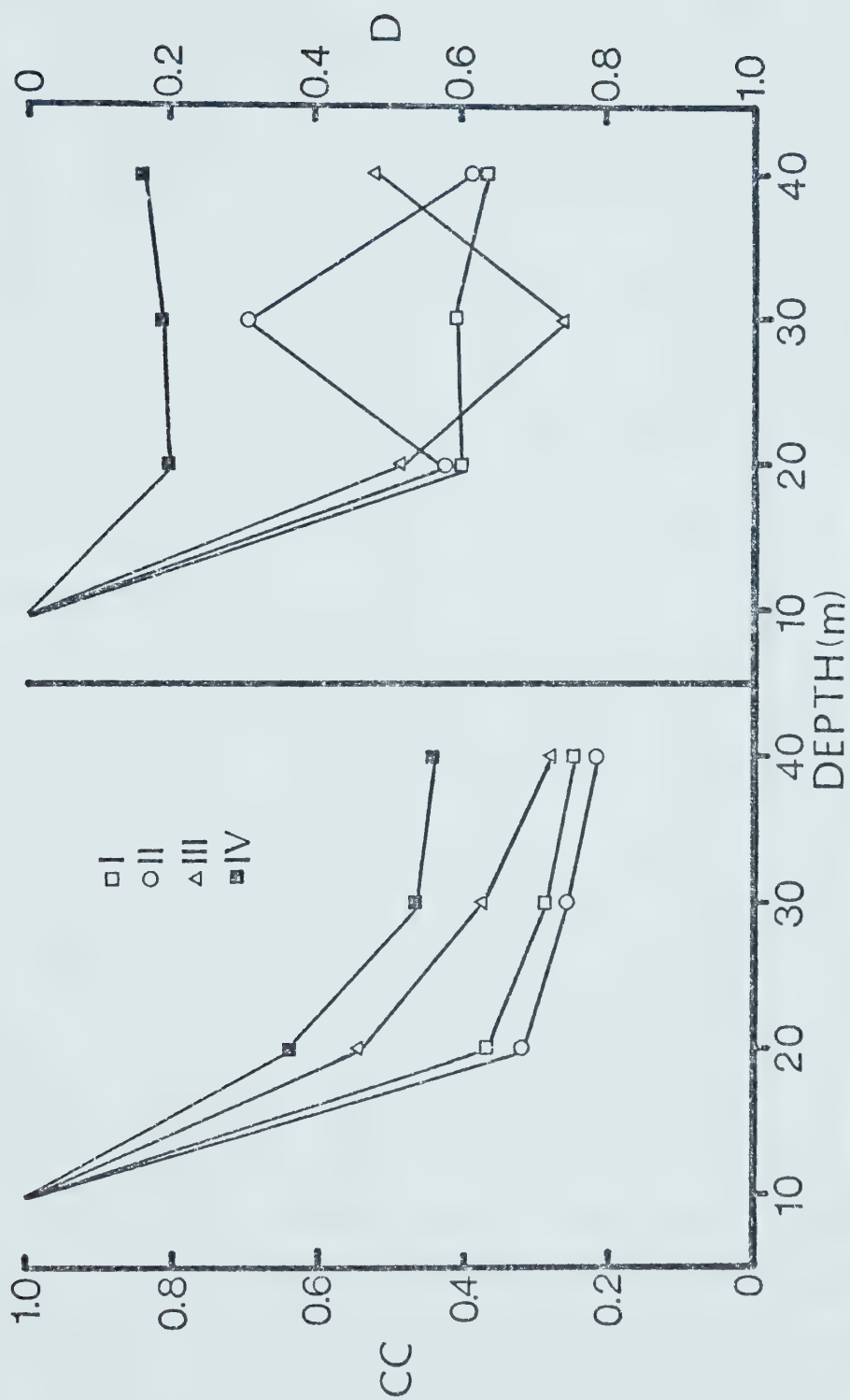


FIG 5 - Comparison of resident community composition along transects by two indices - the coefficient of community (CC) and Euclidean distance (D). The community in each quadrat along each transect is compared to its respective 10 m community.

bers of Coryphopterus personatus in some quadrats (high p_k value) have a marked effect on the value of D and are partially responsible for some of the variability.

It is interesting to note that transects I and II, which were located close together on the reef slope, have very similar CC curves and the D values are almost identical except for 30 m. The D curve of the Bonaire transect is distinctly different from the others, indicating greater homogeneity in community composition along the transect. This finding is supported by the lower beta diversity of the Bonaire transect (Table 4).

If adjacent pairs of quadrats along each transect are compared (Fig. 6), a similar trend is observed along all transects. There is a general tendency for an increase in similarity with an increase in depth i.e. the deeper quadrats are more similar to each other than the shallower ones.

An analysis of the species composition of the quadrats at the beginning of the study (after the first four censuses), as compared with that at the end of the study, revealed some minor differences. I attribute these largely to chance processes. The small changes in the substrates of the quadrats were probably not significant in affecting species composition, although larger changes over a longer period probably would be (e.g. Smith and Tyler 1975). A detailed examination revealed that there were several instances where there was evidence of the "extinction" of a species in a quadrat. These were resident species which could normally be found at that depth. I

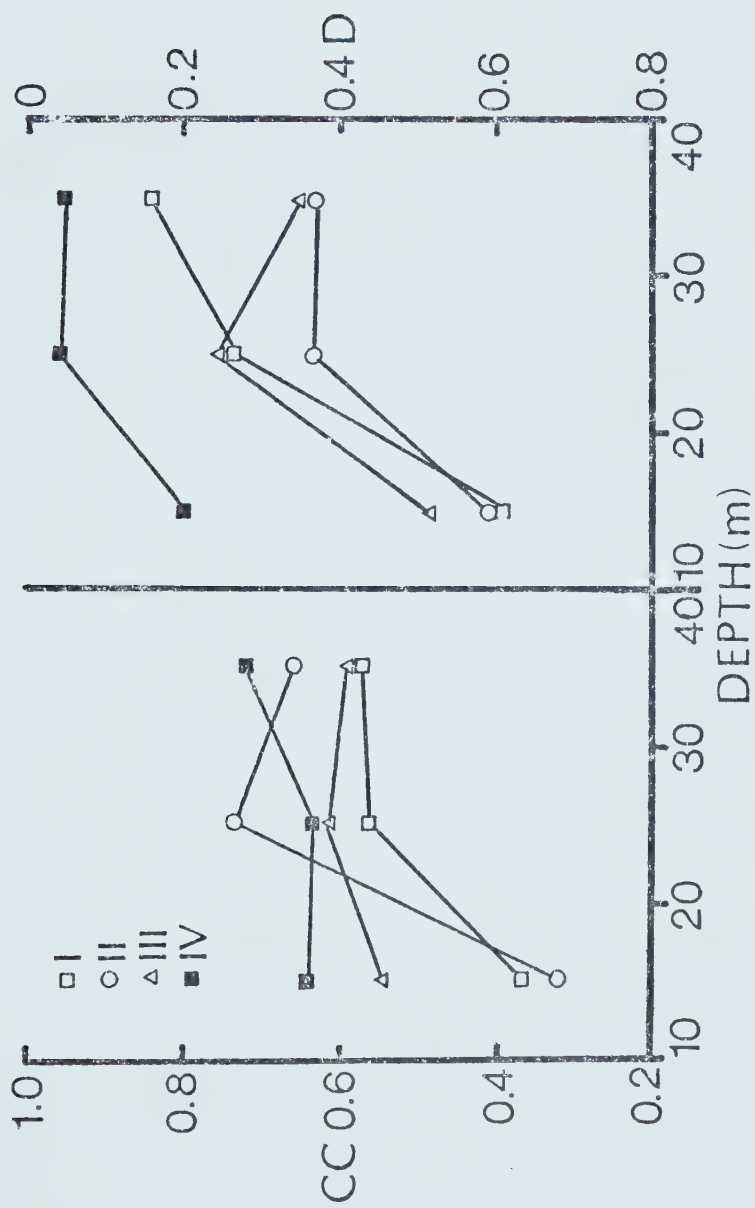


FIG. 6 - Comparison of resident community composition between adjacent pairs of quadrats along each transect by two indices - the coefficient of community (CC) and Euclidean distance (D).

discounted species which were present only as recruits or juveniles and subsequently disappeared. Such occurrences indicate that recruits may have settled in an unsuitable area or that juveniles may have changed habitat as they grew to a larger size. With these restrictions, only three cases of possible "extinction" could be found (Table 6). Acanthemblemaria spinosa has a very limited home range and, as a lone individual, would be unsuccessful in reproducing if it remained in the quadrat. It may simply have left its hole and been eaten by a predator. An explanation of the disappearance of the two other species is more difficult. Apogon phenax was usually represented by one or two individuals; they may have moved to shelter holes outside the quadrat. The disappearance of Gramma loreto after almost one year of continuous residence is perplexing. The maximum number (up to seven) and the occurrence of all three size classes during this period indicates the suitability of the habitat; as such, I have no explanation for their disappearance.

Each species in the study was assigned to a broad trophic category following the outline of Randall (1967). The categories are somewhat arbitrary as most species feed opportunistically and ingest a wide variety of material. The feeding habits of three species, for which no information was available, were determined by gut contents analysis. Table 7 summarizes the trophic composition of the resident community of each quadrat.

The species were also classified according to principal activity period and to one of the three home range cate-

TABLE 6 - Possible "extinctions" of three species during an 18 month period (36 censuses). Only mature Acanthemblemaria spinosa and Apogon phenax were present. All three size classes of Gramma loreto were represented.

Quadrat	Species	Max. no./ census	Censuses present	Censuses absent
I-10	<u>Acanthemblemaria spinosa</u>	1	5/5	30/30
III-40	<u>Apogon phenax</u>	3	10/15	17/17
	<u>Gramma loreto</u>	7	24/24	12/12

TABLE 7 - Trophic composition of fish communities at four depths (10m, 20m, 30m, 40m) along three transects (I, II, III) at Curaçao and one transect (IV) at Bonaire. The number of species in each category is listed and its percentage of the community is given below.

Trophic composition	I				II				III				IV			
	10m	20m	30m	40m	10m	20m	30m	40m	10m	20m	30m	40m	10m	20m	30m	40m
Herbivores	3	2	2	2	2	2	2	2	2	2	2	1	3	2	2	3
	15.8	9.1	11.8	12.5	10.0	7.7	10.5	10.5	7.7	7.1	9.1	6.3	9.4	7.4	8.0	13.0
Omnivores	2	2	1	1	3	2	1	1	2	2	1	1	2	2	1	1
	10.5	9.1	5.9	6.3	15.0	7.7	5.3	5.3	7.7	7.1	4.5	6.3	6.3	7.4	4.0	4.3
Carnivores	3	7	4	3	6	5	3	4	8	6	6	4	7*	9	8	8
	15.8	31.8	23.5	18.8	30.0	19.2	15.8	21.1	30.8	21.4	27.3	25.0	21.9	33.3	32.0	34.8
Planktivores	8	9	8	9	6	13	11	11	10	14	11	9	16	11	12	10
	42.1	40.9	47.1	56.3	30.0	50.0	57.9	57.9	38.5	50.0	50.0	56.3	50.0	40.7	48.0	43.5
Cleaners	1	0	0	0	1	1	0	0	1	1	0	0	2	1	1	0
	5.3	0	0	0	5.0	3.8	0	0	3.8	3.6	0	0	6.3	3.7	4.0	0
Unknown	2	2	2	1	2	3	2	1	3	3	2	1	2	2	1	1
	10.5	9.1	11.8	6.3	10.0	11.5	10.5	5.3	11.5	10.7	9.1	6.3	6.3	7.4	4.0	4.3
Total number resident spp.	19	22	17	16	20	26	19	19	26	28	22	16	32	27	25	23

* includes one piscivore

gories defined earlier, namely rc, rp and r+. The activity period was determined from the diurnal and nocturnal observations as well as from the literature (Starck and Davis 1966; Hobson 1972; Collette and Talbot 1972). The home range classification was based solely on the results of this study but the estimates for most species are in general agreement with those of Smith and Tyler (1972). Using the above classification, it was possible to characterize the community of each quadrat and to make comparisons of these three facets of community structure.

Comparisons were made, both between the four transects and between the four depths, to detect differences in the communities. An analysis of variance of the number of species per quadrat, testing each trophic category separately, showed one significant difference between the transects (carnivores, $F = 5.54$, $p < 0.05$). A similar analysis using the transformed (arc sin) percentage data, also yielded one significant difference (herbivores, $F = 3.70$, $p < 0.05$). In addition, I tested (analysis of variance) for differences between the four depths in each category. No significant differences were found with number of species, but the percentage data for omnivores was significantly different ($F = 5.71$, $p < 0.05$).

The data for the principal activity period and the home range designation (Table 8) were analyzed in the same manner as the trophic data. No significant differences were found in activity period between the transects. Only one category yielded a significant difference when the home ranges

TABLE 8 - Composition of fish communities by principal activity period and home range at four depths (10m, 20m, 30m, 40m) along three transects (I, II, III) at Curaçao and one transect (IV) at Bonaire. The number of species in each category is listed and its percentage of the community is given below.

Activity period	I				II				III				IV			
	10m	20m	30m	40m	10m	20m	30m	40m	10m	20m	30m	40m	10m	20m	30m	40m
Diurnal	15	15	15	12	16	16	13	12	19	19	14	12	21	19	17	16
	78.9	68.2	88.2	75.0	80.0	61.5	68.4	63.2	73.1	67.9	63.6	75.0	65.6	70.4	68.0	69.6
Nocturnal	3	5	1	2	1	9	5	5	5	8	6	3	8	6	6	4
	15.8	22.7	5.9	12.5	5.0	34.6	26.3	26.3	19.2	28.6	27.3	18.8	25.0	22.2	24.0	17.4
Both	1	2	1	2	3	1	1	2	2	1	2	1	3	2	2	3
	5.3	9.1	5.9	12.5	15.0	3.8	5.3	10.5	7.7	3.6	9.1	6.3	9.4	7.4	8.0	13.0
<hr/>																
rc*	7	6	6	7	7	8	6	7	8	7	6	6	10	8	9	8
	36.8	27.3	35.3	43.8	35.0	30.8	31.6	36.8	30.8	25.0	27.3	37.5	31.3	29.6	36.0	34.8
rp*	8	11	8	6	8	11	10	8	9	14	11	6	12	10	8	9
	42.1	50.0	47.1	37.5	40.0	42.3	52.6	42.1	34.6	50.0	50.0	37.5	37.5	37.0	32.0	39.1
r+*	3	5	3	3	4	7	3	4	7	7	5	4	10	9	8	6
	15.8	22.7	17.6	18.8	20.0	26.9	15.8	21.1	26.9	25.0	22.7	25.0	31.3	33.3	32.0	26.1
Sponge-dwellers	1	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0
	5.3	0	0	0	5.0	0	0	0	7.7	0	0	0	0	0	0	0
Total number resident spp.	19	22	17	16	20	26	19	19	26	28	22	16	32	27	25	23

* For explanation see Table 1 and text

were compared; both number of species in r^+ ($F = 7.35$, $p < 0.01$) and percentage ($F = 9.87$, $p < 0.01$) were highly significant.

The analysis of activity periods and home ranges comparing depths yielded no significant differences in the percentages, but two differences in the number of species. The diurnal category was significant ($F = 4.21$, $p < 0.05$) as was rp ($F = 4.35$, $p < 0.05$).

The same analysis was made with only the three transects in Curaçao. There was one significant difference between transects - in the percentage trophic category (herbivores, $F = 6.66$, $p < 0.05$). No significant differences were found in the number of species or the percentages in either the activity period or the home range categories. This indicates that all of the Curaçao transects were very similar in their community organization.

Several significant differences were however, recorded in the comparisons between depths. The most significant of these were the percentage of planktivores ($F = 8.72$, $p < 0.01$) and the rp category ($F = 7.79$, $p < 0.01$).

Discussion

The transects in this study may be viewed as environmental gradients, and the fishes along them constitute a community gradient or coenocline (Whittaker 1972). Only a few studies have discussed the distribution of reef fish species with depth (Gosline 1965; Barnes et al. 1971), but not from a community viewpoint. A considerable amount of work has been done on the avifauna of altitudinal gradients both

at tropical (Diamond 1973; Terborgh and Weske 1975) and temperate (Able and Noon 1976) latitudes. Terborgh (1971) proposed three models to explain the distribution of the avifauna on an altitudinal gradient. The depth gradient provides a similar analogy. Unfortunately, owing to the small number of sample points (4) and the discontinuous nature of the sampling (fixed depths), it was not possible to compare species abundance curves with the theoretical ones suggested by Terborgh. However, the diversity patterns down each transect could be examined.

The N_0 curves in Curaçao were similar and all four curves showed a decrease with depth from 20 to 40 m (Fig. 4). The diversity numbers N_1 and N_2 had very similar patterns along each transect (as expected from their high correlation (Table 3)), but there was considerable variability in the patterns between transects (Fig. 4). The species richness patterns along the transects are the result of several interacting factors - changes in substrate, depth range differences in species, and possibly some environmental factor(s) associated with depth. Able and Noon (1976) found that all three of Hill's diversity numbers decreased up the altitudinal gradients they censused. Terborgh (1971) and Diamond (1973) both found a general decrease in bird species richness with altitude. Competition and changes in vegetation structure seem to be the most important factors determining the distribution of bird species along an altitudinal gradient.

The species composition of quadrats and the changes along the transects were investigated in some detail. There

are at least three factors which will influence the species composition at any given site. The first is the location of the quadrat on the gradient. The site will fall within the depth ranges of some species and not others. At present, little is known about the interaction of factors influencing the depth distribution of most species (Gosline 1965). In addition, the depth range of some reef fishes varies with locality (Colin 1974). Secondly, the nature of the substrate will be of considerable importance as some species have marked substrate and habitat preferences. Goldman and Talbot (1976) have shown that the fish assemblages found in ecologically different regions of the reef show large differences in both composition and biomass. Almost half of the species (49%) were restricted to one habitat. The third factor is chance recruitment and mortality. Sale and Dybdahl (1975) have suggested that the species composition of small areas of reef is best understood in terms of these two phenomena.

The similarity in species composition (CC) of quadrats at the same depth may be explained in at least two ways. The hypothesis may be entertained that most reef fish species are microhabitat specialists; then those quadrats with similar SR values and substrate composition at the same depth would probably have similar species composition. The data generally do not support this hypothesis. High CC values were prevalent at 40 m but not at the shallower depths with similar SR values. In addition, comparisons of the species composition of quadrats with different SR values at different depths produced a number

of low D-values (high similarity). There was no systematic tendency for quadrats with similar SR values to have similar species composition, although this occasionally occurred in quadrats at the same depth. Such findings suggest that most reef fishes are probably not microhabitat specialists. Another explanation of high CC values is that the size of the quadrat (9 m^2) is sufficiently large that chance recruitment alone may provide a considerable proportion of the species normally found at that depth (P.F. Sale, personal communication) thus leading to high similarity values. A possible explanation of high similarity in D values is more difficult as the proportional abundances of the component species must also be similar, and many factors interact to influence abundance.

The lack of significant differences (analysis of variance) in most aspects of community structure in Curaçao, indicate a strong similarity in the fish communities. Some differences with Bonaire were evident but the communities were basically the same at both islands.

Comparisons of the trophic structure of these communities with those of other studies is of limited value because I chose to concentrate on a specific segment (resident) of all of the species present. In addition, most trophic analyses have been made using biomass rather than numbers. I have no estimates of the biomass of any of the species in the study as I did not collect them. Carnivores are usually more diverse than herbivores on the reef and constitute a relatively large proportion of the biomass of a reef fish community. Randall

(1963) found that carnivores comprised almost 60% of the biomass on natural reefs in the Virgin Islands; the figure for an artificial reef in the same area was much higher (89%). Talbot (1965) showed that carnivores made up a similar percentage of his samples on the reefs off East Africa and that herbivores represented only 19% of the biomass. Talbot and Goldman (1972) reported that planktivores constituted over 40% of the biomass of fishes on the seaward slopes of a pseudo-atoll on the Great Barrier Reef, but were much less significant in the lagoon.

The percent composition (by number) of the communities in this study shows that herbivores and omnivores together comprise 12-26% and carnivores 16-35%. The numerically dominant group in all quadrats comprises the planktivores, which make up 30-50% of the community (Table 7). Plankton represents a net import of energy to the reef (Emery 1968), and many species can crop this food source from the current without having to move over the reef to forage. Reef plankton may be an important food source for species hovering close to shelter. Thus, the preponderance of planktivores in the communities is not surprising considering the concentration on species with small home ranges. Davis and Birdsong (1973) have discussed some of the adaptations which have evolved in species which feed in the water column.

Diurnal species form by far the largest percentage of the communities (62-88%); nocturnal species comprise 6-35% (Table 8). The species which are active during both periods

are more difficult to distinguish and constitute a small proportion of the communities. Smith and Tyler (1972) found that 63% of their resident community was diurnally active and 37% was nocturnal; however, 13 resident species were classified as unknown. There is reasonable agreement between these two sets of figures considering the restricted nature of the communities in this study.

The reef zonation in Curaçao differs from that in most areas of the Caribbean (Glynn 1973). There is rarely any back reef area with associated Thalassia beds and, as a consequence, this important nocturnal foraging ground is absent. This is the most probable reason for the absence of large numbers of nocturnally active grunts (Pomadasyidae) and snappers (Lutjanidae). The species in these two families would have a strong influence on the percentage composition of communities in other areas of the Caribbean.

The division of species into conspicuous and cryptic in the "r" category is somewhat artificial but illustrates the point that a significant proportion of the community may, by its behaviour or colouration, be difficult to detect (Table 8). Reef fishes have evolved numerous means of avoiding detection, either as predators or as prey (Ehrlich 1975). These adaptations become apparent when visual censuses are conducted. The r+ category usually makes up less than 30% of the community (Table 8), as would be expected from the concentration on species with limited home ranges.

Nocturnal communities

The nocturnal habits of coral reef fishes have been documented in several studies (Hobson 1965, 1968; Starck and Davis 1966). The diurnal-nocturnal changeover patterns in reef fish communities have been described in some detail by Collette and Talbot (1972). All of these observations confirm that there are dramatic changes in the appearance and species composition of nocturnal fish communities. In general, the reef has a drab appearance at night as the colourful, diurnal species are replaced by the primarily reddish or silver nocturnal species.

There is apparent a replacement of one group of species by another. During the day, aggregations of planktivores feed at various heights above the reef; Chromis cyaneus and C. multilineatus pick individual plankters two to four meters above the substrate, while large aggregations of Coryphopterus personatus hover within 50 cm of shelter taking reef plankton (Davis and Birdsong 1973). Groups of Clepticus parrai move along the reef face, well above the substrate, feeding on planktonic organisms. On the deeper reef, Chromis insolatus and C. scotti pick plankters from the water column. As night approaches, these aggregations break up and the individuals seek shelter in crevices in the reef. All of these species can be found at night, mainly under ledges, but individuals of Coryphopterus personatus are very difficult to detect despite their abundance.

After dark, the species of two families, the Apogonidae

and the Holocentridae, leave their shelter sites and replace the diurnal planktivores. Phaeontyx conklini moves up high in the water column (2-3m) to feed on plankton while Apogon townsendi appears to feed somewhat lower (1m). The remaining species of apogonids stay within about 25 cm of the substrate. Myripristis jacobus often joins P. conklini in the water column as does the priacanthid, Priacanthus cruentatus. Two other species of holocentrid, Holocentrus marianus and Plectrypops retrospinis remain closer to the substrate (within 25-40 cm). They feed on crustaceans, mainly crabs and shrimps (Randall 1967). The latter species is often seen under a ledge or at a cave entrance, very close to its diurnal shelter site.

One of the most striking features of the nocturnal communities was the abundance of non-resident planktivores sheltering in crevices in the quadrats. Two species were particularly common, Chromis multilineatus and Clepticus parrai. A third species, Paranthias furcifer was recorded mainly along transect III, but was nowhere abundant. Chromis multilineatus was abundant during the day at the shallower depths, particularly along the drop-off (10m), but its numbers decreased rapidly with depth. It was infrequently seen below 30 m. The nocturnal pattern was similar. It was most numerous at 10 m and its abundance showed a steady decrease with depth (Fig. 7). None were recorded at 40 m. The small number at I-10 (Fig. 7) was undoubtedly due to the lack of suitable shelter sites.

No Clepticus parrai were observed at night at 10 m, but they were recorded from the three greater depths. Starck

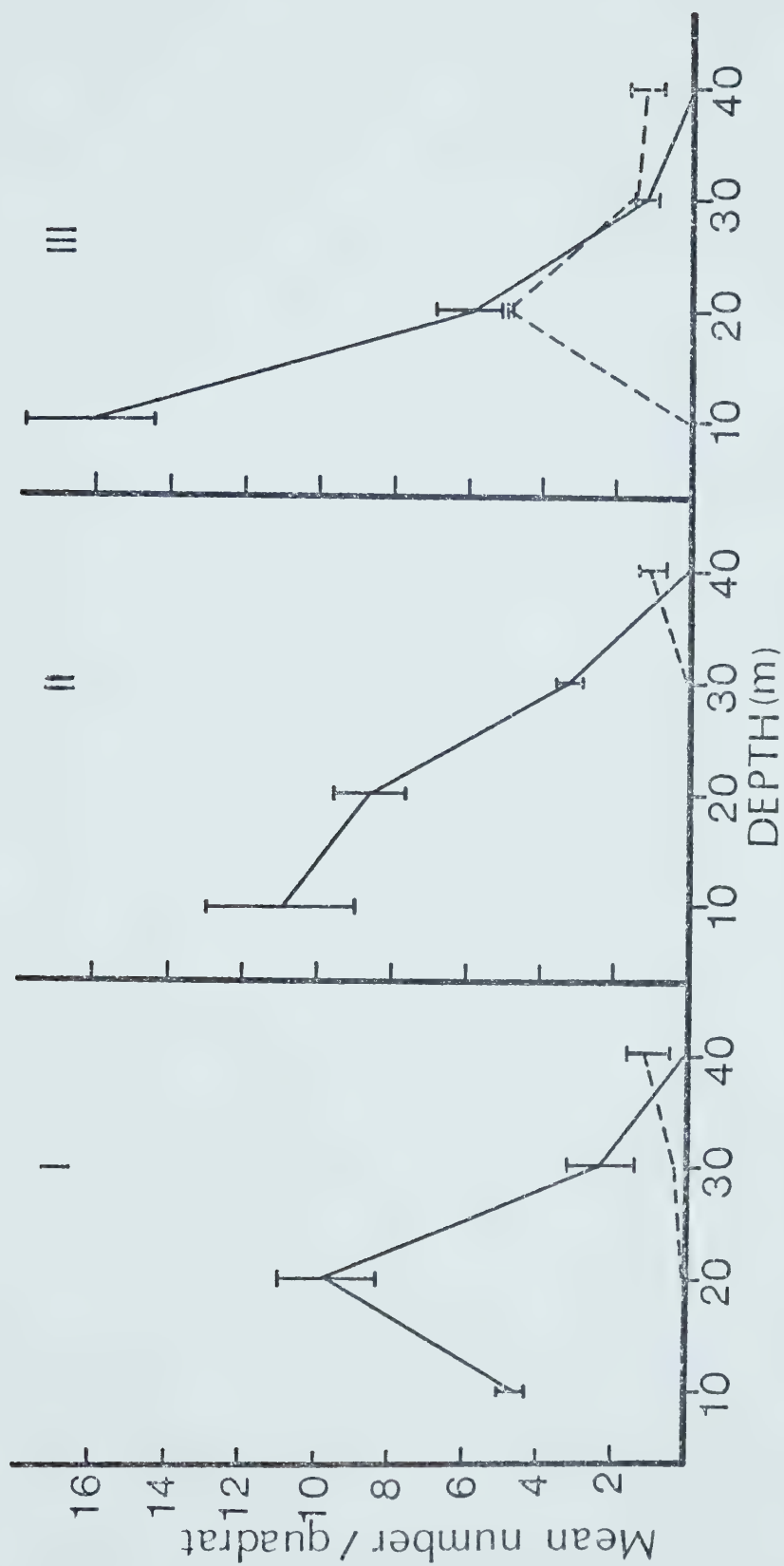


FIG. 7 - Mean nocturnal density of *Chromis multilineatus* (—) and *Clepticus parrai* (--) along three transects (I, II, III) at Curaçao. The bars represent ± 1 SE.

and Davis (1966) found this species sheltering in crevices at night only on the deeper reef (28 m). The number of C. parrai in any quadrat is generally small. This is probably due to its size, as it is a larger species than Chromis multilineatus and requires much larger ledges or holes in which to shelter. Its abundance in any quadrat is, therefore, partially the result of the number of appropriate shelter sites.

The data from transects I and II (Fig. 7) suggest that there might be some depth segregation between the two species, but transect III shows considerably higher numbers of Clepticus parrai at the shallower depths (20 m). The pattern is thus probably the result of local abundance and the normal depth preferences of the two species, not active segregation. In addition, C. parrai was far more abundant during the day at transect III than at the two other transects.

The nocturnal abundance of the apogonids was considerably higher than that observed during the day (Table 9). It was difficult to obtain reasonable nocturnal estimates of abundance for some species because they were high in the water column e.g. Phaeoptyx conklini; thus, only the species remaining within about 1 m of the substrate were considered. Apogon lachneri was the most abundant species on all three transects and was recorded in every quadrat but one (I-10). It was observed in only five quadrats on a regular basis during the day. This is probably because of its preference for deep holes and caves in the reef where it is not easily detected; thus the lower diurnal values (Table 9). Phaeoptyx conklini has a similar microhabitat preference. Livingston (1971) found both of these species

TABLE 9 - Mean diurnal (D) and nocturnal (N) number per quadrat of four apogonid species along three transects (I, II, III) at four depths (10m, 20m, 30m, 40m) at Curaçao. Diurnal values are based on 36 censuses and nocturnal values on 3 censuses.

Species	Period	I				II				III			
		10m	20m	30m	40m	10m	20m	30m	40m	10m	20m	30m	40m
<u>Apogon lachneri</u>	D	-	-	-	-	-	0.5	0.2	0.3	-	1.6	0.8	-
	N	-	7.3	3.7	1.5	0.7	4.3	2.7	3.0	1.7	4.7	6.0	5.7
<u>A. maculatus</u>	D	1.0	-	-	-	0.4	-	-	-	0.4	0.2	-	-
	N	2.0	-	-	-	3.3	-	-	-	1.7	-	-	-
<u>A. phenax</u>	D	-	0.4	0.7	0.3	-	1.2	0.8	0.4	-	0.5	1.0	0.4
	N	-	3.0	3.3	1.0	-	3.0	2.3	-	-	1.3	1.3	-
<u>A. townsendi</u>	D	5.3	4.0	-	-	-	1.4	0.1	0.3	0.8	5.9	0.1	-
	N	1.0	1.7	-	-	6.3	-	1.0	-	4.7	-	-	-

deeper in holes or caves than other apogonids and determined that Apogon lachneri often did not leave its cave at night to feed. Collette and Talbot (1972) reported A. lachneri feeding close to the substrate and within a few meters of its daytime cave. My observations are in general agreement with these authors. Another species, Apogon phenax, not reported by these authors, was found to remain very close (15 cm) to the substrate and within about 50 cm of its diurnal shelter cave. Several sites known to be diurnally occupied by A. phenax were specifically examined at night, and they invariably had an individual close to the site or at the cave entrance.

Another species frequently seen foraging near the substrate was the grammistid, Rypticus subbifrenatus. It was usually found close to the site where it was observed diurnally. Starck and Davis (1966) also reported this species to be active at night.

Maps of each quadrat were carried during the censuses so that it was possible to mark the location of many species during subsequent observations. A number of shelter sites were consistently used by the same species, presumably the same individuals, over a period spanning four to five months.

NUMERICAL ASPECTS OF COMMUNITIES

Recruitment patterns

Recruitment is a process of considerable ecological significance, but little work has been done in the coral reef biotope to elucidate this process. As Smith and Tyler (1975) have pointed out, there is a "generally recognized seasonal superabundance of recruits" on the reef, but the patterns of abundance have not been documented. As part of this study, I have investigated the abundance and periodicity of post-larval recruits along the three transects in Curaçao. Little is known about the early life history of most tropical reef fishes; therefore, the recruit size limits which I have defined (Table 10), are somewhat arbitrary. They do, however, provide a useful working base for monitoring recruitment in the field.

In order to demonstrate seasonality, a minimum of two annual cycles is required. Although some recruitment data are available from January 1974 onward, recruit counts are available for all 12 quadrats only from May 1974 to June 1975. Since these data span only 14 months, it is not possible to comment adequately on seasonality. However, the data show that recruitment does occur throughout the year in a number of species and that there are definite peaks in numerical abundance which suggest a seasonal pattern.

In some species, no recruits were ever observed and in others, the numbers were too meager to determine any trends. If a total of less than 20 recruits was recorded for a species, it was excluded from the analysis. Adequate

TABLE 10 - Designated size limit of recruits

Family	Species	Size limit (Total length in mm)
Serranidae	<u>Petrometopon cruentatum</u>	< 70
Grammidae	<u>Gramma loreto</u>	< 20
Apogonidae	<u>Apogon lachneri</u>	< 20
	<u>A. townsendi</u>	< 20
	<u>Phaeoptyx conklini</u>	< 20
Sciaenidae	<u>Equetus</u> sp. (<u>punctatus</u> ?)	< 20
Pomacentridae	<u>Chromis cyaneus</u>	< 25
	<u>C. insolatus</u>	< 25
	<u>Eupomacentrus partitus</u>	< 20
	<u>E. planifrons</u>	< 20
Gobiidae	<u>Coryphopterus glaucofraenum</u>	< 15
	<u>C. lipernes</u>	< 10
	<u>C. personatus</u>	< 10
	<u>Gnatholepis thompsoni</u>	< 15
	<u>Gobiosoma evelynae</u>	< 15
Canthigasteridae	<u>Canthigaster rostrata</u>	< 20

recruitment data were available for 16 resident species from seven families. As the number of recruits of a species in any given quadrat is generally small, it is difficult to detect trends; therefore, I have combined the data from all 12 quadrats. The figure for each species thus illustrates the overall pattern of recruit occurrence and abundance along a section of fringing reef. There is considerable variation in the relative abundance of recruits between quadrats and between depths (Table 11), but, in general, the recruitment peaks in a species are similar in the time of occurrence at different depths. Some of the factors which may influence distribution and abundance of recruits are substrate variability, patchiness in the plankton and competitive displacement. At present, it is not possible to define the parameters which determine recruitment success at any given location on the reef.

One factor which will have affected the recruit abundance pattern is the inclusion of the same individuals in more than one census. This is likely to have occurred as I chose to concentrate on the non-labile species. As none of the fishes were marked, it is not possible to estimate the extent to which this facet of the technique has influenced the observed pattern. I assume that considerable numbers of recruits are lost to predation and that the survivors rapidly grow into the next size category. Growth rates of 0.3 to 0.8 mm per day have been recorded in several subtropical species (Houde 1974). Allen (1975) lists growth rates in the

TABLE 11 - Number of recruits recorded at four depths (10m, 20m, 30m, 40m) along three transects (I, II, III) at Curaçao for the period May 1974 to June 1975.

Species	10 m				20 m				30 m				40 m				Recruit total
	I	II	III	Depth total	I	II	III	Depth total	I	II	III	Depth total	I	II	III	Depth total	
Serranidae																	
<i>P. cruentatum</i>	1	14	3	18	—	4	—	4	2	—	4	6	4	5	3	12	40
Grammidae																	
<i>G. loreto</i>	—	—	—	—	2	57	17	76	19	26	69	114	2	20	5	27	217
Apogonidae																	
<i>A. lachneri</i>	—	—	—	—	—	8	4	12	—	2	6	8	—	2	—	2	22
<i>A. townsendi</i>	64	3	13	80	33	3	51	87	—	3	1	4	—	—	—	—	171
<i>P. conklini</i>	2	—	4	6	8	2	18	28	5	1	—	6	—	4	—	4	44
Sciaenidae																	
<i>E. punctatus</i>	7	2	1	10	—	14	—	14	4	1	1	6	1	—	2	3	33
Pomacentridae																	
<i>C. cyanea</i>	63	—	—	63	18	2	37	57	—	—	7	7	—	—	—	—	127
<i>C. insolatus</i>	—	—	—	—	—	—	9	9	—	2	24	26	—	2	8	10	45
<i>E. partitus</i>	317	116	130	563	74	9	57	140	10	7	8	25	1	3	3	7	735
<i>E. planifrons</i>	57	11	3	71	—	—	—	—	—	—	—	—	—	—	—	—	71
Gobiidae																	
<i>C. glaucifrenum</i>	58	361	57	476	265	115	93	473	282	199	39	520	94	94	30	218	1687
<i>C. lipernes</i>	23	15	12	50	91	149	87	327	49	29	57	135	16	10	33	59	571
<i>C. personatus</i>	5	—	10	15	810	1145	1325	3280	130	130	1810	2070	5	520	165	690	6055
<i>G. thompsoni</i>	148	276	77	501	213	49	105	367	110	154	40	304	72	71	14	157	1329
<i>G. evelynae</i>	4	2	10	16	4	9	9	22	3	1	—	4	—	1	—	1	43
Canthigasteridae																	
<i>C. rostrata</i>	10	10	11	31	24	14	31	69	11	13	28	52	1	3	13	17	169

juveniles of several pomacentrid species of up to 13 mm per month. It is probable, therefore, that most of the species in this study would grow out of the recruit size category in the period spanned by one or two censuses.

Ideally, many annual cycles are needed to determine the consistency of a pattern and the degree of variability, but some trends can nonetheless be detected in the data. Unfortunately, no quantitative recruitment data are available for most species during the spring peak (March-April) of 1974. The field observations and some data indicate that there was a recruitment period in most of the species at this time, but it appears to have been of smaller magnitude than that of April 1975.

The recruitment data from Bonaire are not included in the figures as the numbers are based on only one transect censused at three to four month intervals and are therefore not strictly comparable with Curaçao. However, the pattern of occurrence observed in Bonaire is mentioned whenever sufficient data are available for a species.

Serranidae

Despite the large number of species within this important family, data are available for only one species.

Petrometopon cruentatum a common, small grouper on Curaçao reefs, had recruits present at all depths, although the numbers were highly variable (Table 11). No pattern is apparent except that recruits appear to be more common in the winter and spring (Fig. 8a). Munro et al.(1973) reported

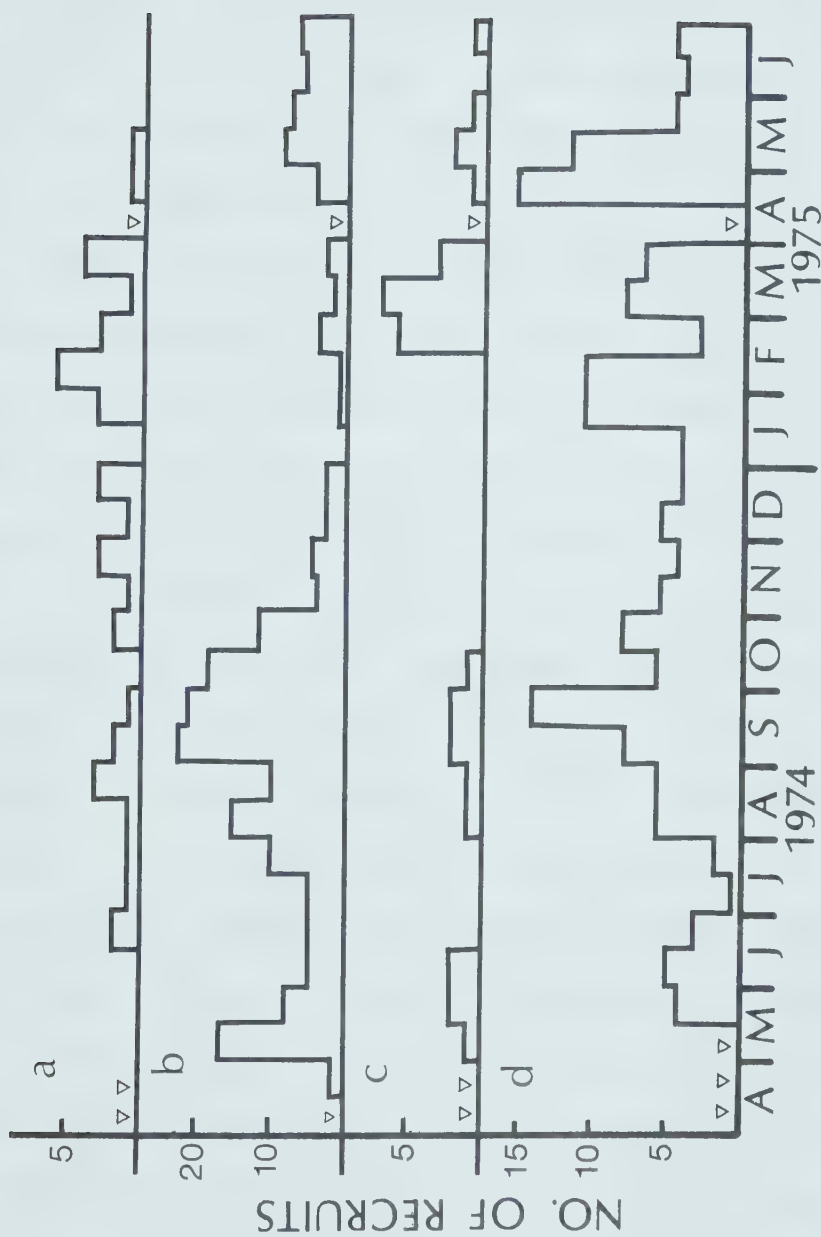


FIG. 8 - Recruit abundance patterns of four species (a) *Petrometopon cruentatum*, a serranid, (b) *Gramma loreto*, a grammid, (c) *Equetus punctatus*, a sciaenid and (d) *Canthigaster rostrata*, a canthigasterid. Triangles indicate periods for which no data are available.

ripe fishes from Jamaica in the period from February to June with a maximum in March. I have designated the recruit size limit as 70 mm total length (TL), which is much larger than that given for the other species. This figure was chosen as individuals less than about 30 mm TL have never been observed in the field. Thompson and Munro (1974) state that groupers smaller than 50 mm TL were never observed in the field by their group in Jamaica. Individuals up to 70 mm may be as much as one year old.

The smallest individuals observed were always found hiding under ledges and were usually very difficult to detect. I monitored the presence of one individual (about 50 mm TL) under the eroded base of a colony of the coral Montastrea annularis for a period of four weeks. The site was checked during the biweekly census of the quadrat. An individual, presumably the same one, was found in precisely the same position for three consecutive censuses. Predatory behaviour was observed on several occasions. The individual attempted to capture recruit-sized sand-dwelling gobies (e.g. Gnatholenis thompsoni and Coryphopterus glaucofraenum) by lunging at them from under the ledge when they approached within 15 to 20 cm. On at least one occasion, it was successful and appeared to swallow its prey whole. It returned to its position under the ledge immediately after capturing the prey.

Grammidae

The members of this family are small, often brightly coloured fishes which remain close to cover and dive into

small shelter holes when disturbed.

Gramma loreto is a planktivore which is commonly found in caves and under ledges. Recruits were present throughout most of the year. No individuals were observed in the 10 m quadrats, probably because the substrates were unsuitable; however, considerable numbers were present in the 10 m quadrat in Bonaire. The period of greatest abundance was September with evidence of another peak in May (Fig. 8b). Few recruits were present from November to April. The pattern of abundance in Bonaire was similar to that observed in Curaçao.

Apogonidae

The apogonids are nocturnally active fishes which shelter by day in crevices and caves in the reef. Due to their secretive habits, it is not possible to obtain an accurate estimate of their abundance by visual censusing alone. As previously mentioned, poisoning was precluded; therefore, it must be assumed that apogonids were present in greater abundance than were detected and that recruits were probably present at times of the year when none were recorded. Nonetheless, it is significant that the three species for which data are available all provide evidence for a bimodal recruitment pattern.

Apogon townsendi had recruits at all depths except 40 m (Table 11). There is a marked bimodal pattern with a spring peak in April-May and an autumn peak in September (Fig. 9c). Few individuals were observed in the intervening

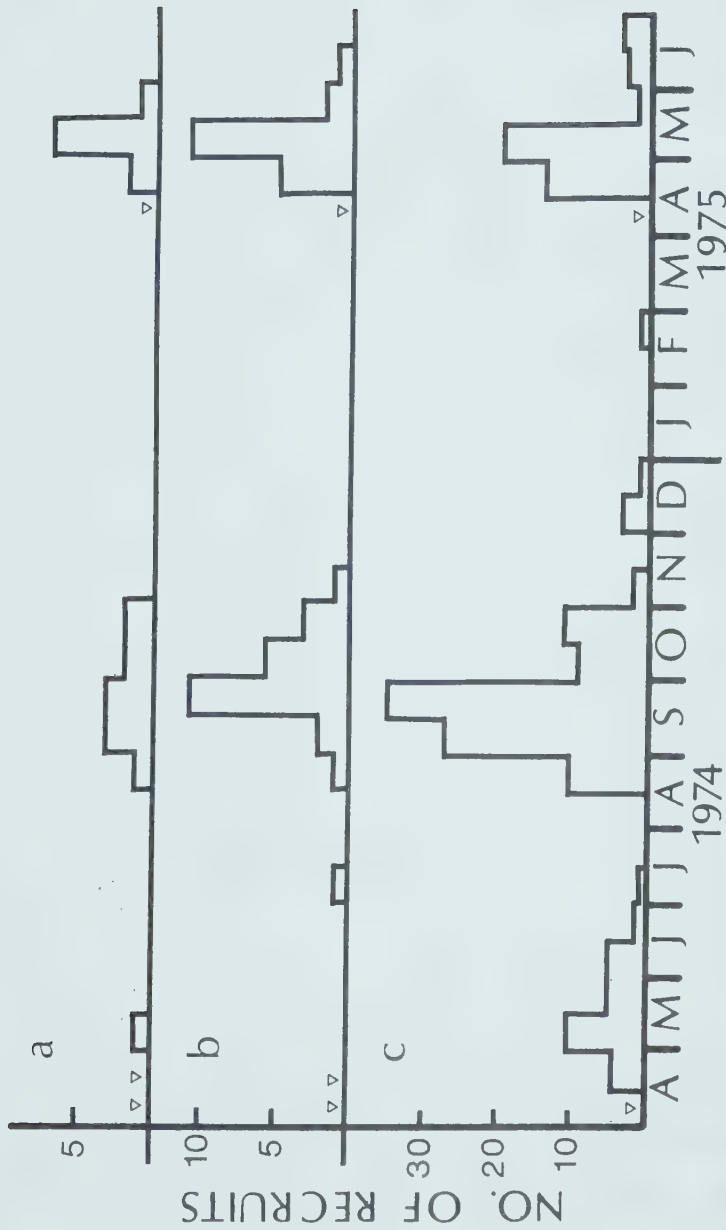


FIG. 9 - Recruit abundance patterns of three apogonid species (a)

Apogon lachneri, (b) Phaeoptyx conklini and (c) A. townsendi.

Triangles indicate periods for which no data are available.

period.

Phaeoptyx conklini had considerably fewer recruits, but peaks are evident in September and May (Fig. 9b). No recruits were observed from November to April. Charney (1976) found the greatest abundance of recruit-sized individuals (< 21 mm standard length (SL)), in poison samples from the Bahamas, in March and April of several years. Samples for all months were not available.

The numbers of Apogon lachneri are small, but again there is a suggestion of a bimodal pattern (Fig. 9a). No recruits were recorded at 10 m in Curaçao but some were present at this depth in Bonaire in September.

Powles (1975) found two peaks in the abundance of larval apogonids around Barbados, one in March-April, and the other in September-October. Recruit-sized individuals of four common apogonid species have been found throughout the year in extensive poison collections from the Bahamas, indicating the possibility of year-round reproduction (George Dale, personal communication).

Sciaenidae

Only four species in this family are commonly associated with coral reefs in the Caribbean (Randall 1968). Of these, three are species in the genus Equetus. The recruits of the spotted drum, E. punctatus, and the cubbyu, E. acuminatus, are difficult to distinguish in the field at sizes less than 20 mm TL. As E. acuminatus was only rarely seen in the study area and E. punctatus was a fairly common species, I

have assumed that most of the recruits were from the latter species.

The recruits of E. punctatus were recorded from all depths but were more common in the shallower quadrats (Table 11). Although the sample size is small, there is a clear peak in February-March (Fig. 8c). Munro et al. (1973) found ripe fishes in April, July and September and Erdman (1956) reported ripe fishes in August.

Powles (1975) has presented evidence which suggests that the larvae of some Equetus species may be epibenthic. He found a larval E. acuminatus, only 6.6 mm SL which had a strong substrate-oriented response when displaced. It still had not completely metamorphosed to the juvenile form. Very small (<15 mm TL) Equetus spp. have been observed actively maintaining station close to the substrate; they remained in the same location for several weeks.

Pomacentridae

Pomacentrids comprised a substantial proportion of the communities and were particularly abundant in the shallower quadrats. Recruitment data are available for four species.

Eupomacentrus partitus provides the most convincing evidence of year round recruitment in the pomacentrids. Recruits were present throughout the year at 10 m and for most of the time at 20 m. Few recruits occurred at the greater depths (Table 11). There is a marked bimodal recruitment pattern with peaks occurring in September and April (Fig. 10d). The few recruits recorded at 30 and 40 m appeared at these

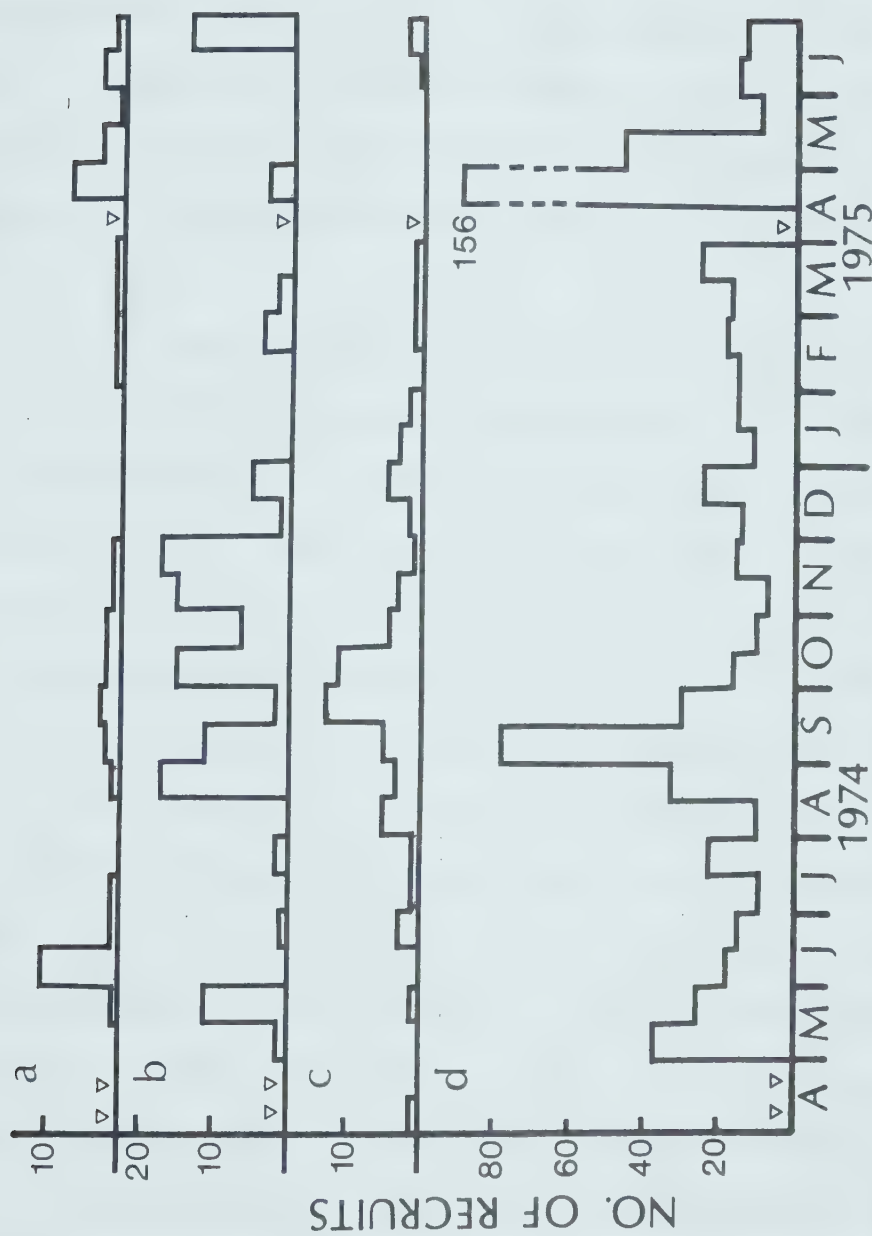


FIG. 10 - Recruit abundance patterns of four pomacentrid species

(a) Chromis insolatus (b) C. cyaneus (c) Eupomacentrus planifrons
 (d) E. partitus. Triangles indicate periods for which no data are available.

peak times.

Recruits of E. planifrons were only observed at the 10 m quadrats and the majority were found in only one quadrat (Table 11). There is a clear peak in September-October with few individuals present during the rest of the year (Fig. 10c). The spring period of March to May has few or no recruits. Thresher (1976) reported very little reproductive activity in the spring (April-May) in this species in the Florida Keys.

The data for Chromis cyaneus do not provide evidence of the year round presence of recruits, although this may be an artifact of their patchy distribution (Table 11). The largest numbers occur in the period from August to November, while other peaks occur in May and June (Fig. 10b). Most of the recruits were present at the shallower depths. The only period of abundance of recruits in Bonaire was May, 1975.

The recruits of Chromis insolatus occur mainly at 30 and 40 m (Table 11). They tend to form aggregations, and their distribution is patchy as is that of C. cyaneus. Peaks may be discerned in June and in the following April, with low numbers at other times (Fig. 10a). Recruits were present in about equal numbers in February and May in Bonaire.

Powles (1975) found peaks in pomacentrid larvae in September-October in two consecutive years around Barbados. The period from January to June of one year was characterized by irregular but high catches with peaks in March and June.

Gobiidae

The small size and often cryptic colouration of the numerous species in this family limit observations of recruitment to those species which, by substrate preference or behaviour, may be readily counted.

Coryphopterus lipernes is a particularly suitable species in which to follow recruitment. It is most often found resting on live coral (Colin 1973) and because of its striking colouration, even very small individuals (<10 mm TL) may be readily observed. Recruits were present throughout the year and were most abundant at 20 m (Table 11). Several peaks may be distinguished during the year and these recruitment peaks generally occurred in the same month at different depths. The largest peak was in March with others in May and June. There is also a broad period of abundance between August and November (Fig. 11a). July and January-February appear to be periods of low recruit abundance. The numbers in Bonaire showed basically a similar pattern in corresponding months.

Coryphopterus personatus is a common species which characteristically forms aggregations and hovers within 50 cm of the substrate. Large aggregations composed of recruits and juveniles, but with few mature individuals, were frequently seen close to shelter. Few recruits were observed at 10 m, probably due to the lack of suitable outcrops for shelter. They were, however, abundant at this depth in Bonaire where the greater vertical relief provided adequate cover. Aggrega-

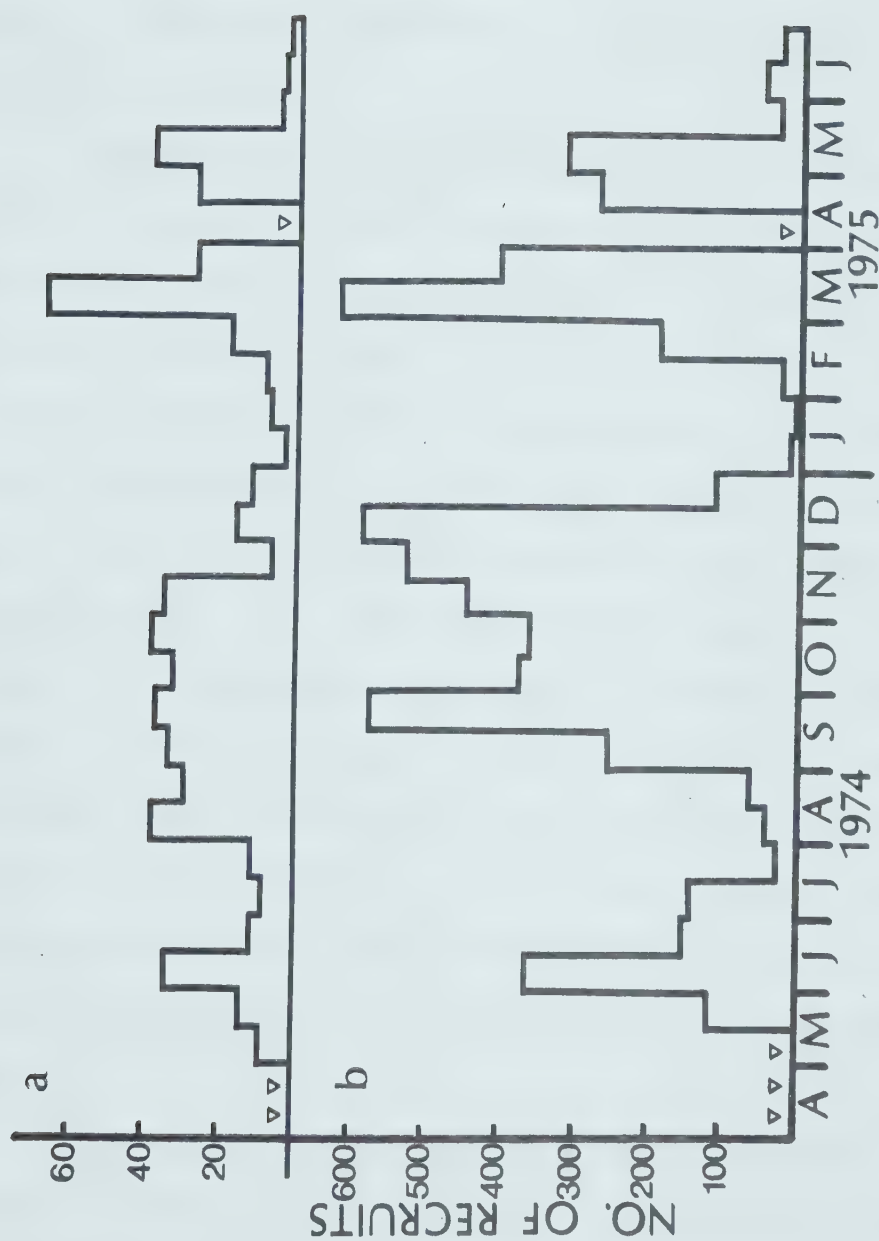


FIG. 11 - Recruit abundance patterns of two gobiid species

(a) *Coryphopterus lipernes* (b) *C. personatus*. Triangles indicate periods for which no data are available.

tions were present throughout most of the year, but several peaks may be distinguished. There is a period of relatively high abundance from September to December and a spring peak in March (Fig. 11b). Another peak occurs in May-June. July-August and January-February are periods of low recruit abundance. The numbers observed in Bonaire corresponded closely with this pattern.

Coryphopterus glaucofraenum is an abundant sand-dwelling species. Two closely-allied species (C. eidolon Böhlke and Robins and C. thrix Böhlke and Robins) are also frequently found on sand. A number of collections were made in sandy areas adjacent to the quadrats to determine the presence and abundance of these other species. Seventy-five percent of the individuals collected were identified as C. glaucofraenum. The remainder were C. thrix. As it was not possible to distinguish recruits of these two species in the field, I have included all recruits under C. glaucofraenum assuming that the majority were from this species. In addition, the recruit numbers were underestimated as individuals of such small size are difficult to count, and with their hyaline appearance, blend extremely well with the sandy substrate.

Recruits were present the year round but there were marked differences in abundance. Peaks occur in September-October and April-May (Fig. 12c). There is a considerable difference in the numbers observed in June of the two consecutive years. As in the two preceding species, recruit abundance

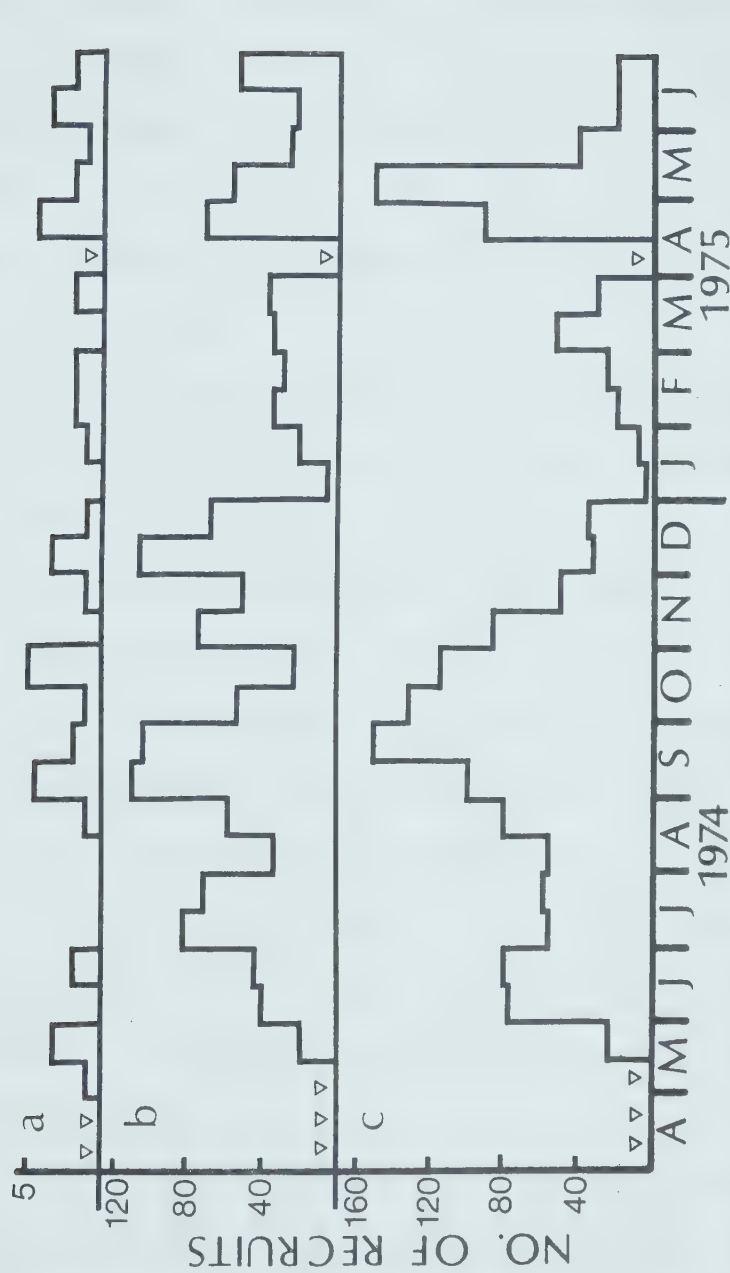


FIG. 12 - Recruit abundance patterns of three gobiid species

(a) *Gobiosoma evelynae* (b) *Gnatholepis thomsoni* (c) *Coryphopterus glaucofraenum*. Triangles indicate periods for which no data are available.

is lowest in January-February.

Another frequent inhabitant of sandy substrates, Gnatholepis thompsoni, is often found together with C. glaucofraenum. Again, recruits were present throughout the year. Peaks in abundance are not as clearly defined as in other species; however, four peaks are apparent. They are in July, September, December and April (Fig. 12b). The numbers from January to March are comparatively low in relation to the rest of the year.

One of the obligate cleaning gobies Gobiosoma evelynae is frequently observed on live coral throughout the reef biotope. The bright yellow stripes on its black body contrast well with a coral background. It commonly shares space with Coryphopterus lipernes (Colin 1973) and I have often observed these two species together on the same coral head.

Recruits were present during most of the year (Fig. 12a), but with the small sample size, no peaks can be discerned. Colin (1973) reported the occurrence of small juveniles in March, April, June and July at several islands in the Caribbean. He further suggested that this species may spawn the year round.

The larval catch rates of Powles (1975) indicate that the Gobiidae may have a different pattern of abundance relative to most other inshore fish families. Larval peaks occurred in the spring and autumn as well as in December-January and in June. Low numbers were recorded in July-August. It is difficult to draw comparisons between the pattern of a

single species and that of a speciose family such as the Gobiidae. However, it does seem apparent that some members of the Gobiidae have more than two peaks per annual cycle.

Canthigasteridae

The puffer, Canthigaster rostrata, is found in a wide variety of habitats, and is frequently observed in reef areas. Recruits remain very close to shelter and are normally found hovering under ledges or in depressions in the reef. Recruits were observed in all months of the year. Peaks may be detected in September, January-February and April (Fig. 8d). Recruits were only evident in Bonaire in May.

Discussion

Smith and Tyler (1972) suggested that recruitment into reef fish communities would be found to be intermittent throughout the year with seasonal cycles of abundance, when communities were studied over at least one annual cycle. The data presented here, which span 14 months, indicate that recruitment in most species does show seasonal cycles in abundance. They also show that there are marked differences in recruit abundance at three transects along a small section of the coast (Table 11) and at different depths. Many of these differences can probably be attributed to substrate variability, although many other factors undoubtedly play an important role. It will be necessary to learn much more about the larval ecology of reef fishes in order to understand the factors affecting larval settlement and recruit distribution. Data on delayed transformation of pelagic larvae will be

essential in this regard.

There is considerable variability in recruit abundance in several species (e.g. Coryphopterus personatus (Fig. 11b)) in the months of overlap of data, viz. May and June 1974 and 1975. There is no obvious explanation for such large differences. Allen (1975) states that periodic "blooms" may occur in some coral reef fishes in seasons when favourable environmental conditions enhance recruit survival. These differences may be the result of such a bloom. Powles (1975) found considerable differences in larval catch rates in the same months of two consecutive years in a number of reef fish families.

In seven of the 16 species studied, there is clear evidence that recruits were present essentially throughout the year. These are the species with the largest sample sizes (Table 11). The remaining species, for which far fewer numbers were recorded, had periods when no recruits were observed in the quadrats. I suggest that most, if not all, of these species will be found to have year round recruitment as well when the sample sizes are increased and other sampling techniques are used. Juveniles (the next largest size category) of most of these species were recorded in almost all months of the year, thus indicating that recruitment had occurred earlier.

There appear to be two principal peaks in the recruit abundance pattern of most species, one in the spring (March-May and one in the autumn (September-November). Pearse (1974)

has suggested on limited evidence that such a pattern might be observed in species near the equator. These peaks in recruitment are presumably owing to a large proportion of the population spawning at an earlier time. The year-round presence of recruits further indicates that some spawning probably occurs throughout the year in these species. This assumption may not be entirely valid as differential growth rates under various competitive and environmental regimes will distort the pattern. Reproductive periodicity in a species is best determined by the sampling of the population throughout the year and the examination of the reproductive condition of the gonads.

Powles (1975) concluded on the basis of larval catch rates, that most of the inshore reef fish families around Barbados had two peaks in abundance in the ichthyoplankton, one in March-May and one in August-October. Assuming a larval period of three to four weeks for most species, there is good correspondence between Powles' findings and the data presented here. Moran and Sale (1977) have estimated the "pre-settling" period of a temperate pomacentrid species to be 4 - 6 weeks based on field data.

Munro et al. (1973) determined that the majority of the species they studied in Jamaica spawned in the spring (February-April) when water temperatures were minimal, but there was evidence of year-round spawning in a number of families. Minimum water temperatures also occur in the spring in Curaçao (Fig. 1). Russel et al. (1974) showed that recruitment to a series of artificial reefs on the Great Barrier Reef was

strongly influenced by the time of the year in which the reefs were established. There was heavy colonization by juveniles during the summer, but the numbers were significantly lower during the winter. They indicated that most of the species at their site had a reproductive period of about six months (during the summer) and that recruitment by newly-metamorphosed juveniles reached a peak in mid-summer. These data seem to indicate that there is only one main recruitment peak per year, but, as in the Caribbean, some recruits are present the year-round.

Temporal analysis of community parameters

The community parameters N_0 , NCP, N_1 and $E_{2.1}$ were analyzed to detect possible changes in community structure during the study. These four parameters include all of the significant aspects of community structure: species richness, number of individuals, diversity and evenness. The fluctuations of these parameters over 18 months may be examined to determine if there are any seasonal trends.

A scattergram of each of these parameters against time (in weeks) was plotted for every quadrat in Curaçao. NCP was the only parameter which consistently showed evidence of seasonality. The remaining three parameters showed either linear trends, or apparently random fluctuations. Initially, simple linear regressions were calculated for all parameters in each quadrat. These regressions provided a regression sum of squares (SS) (explained variation) and an F value for a linear fit to the data. To test for the significance of deviations from linearity (seasonal or random changes), stepwise polynomial regression was used. I infer from Box and Jenkins (1970) that a minimum of 4-5 cycles is required for a time series analysis; therefore, this technique was not used as 18 months data were considered insufficient.

A fourth degree (quartic) polynomial was chosen after an inspection of the scattergrams indicated that not more than $1\frac{1}{2}$ cycles (3 inflections) were probably present for any parameter. The number of inflections in a polynomial regression is one less than the degree of the polynomial. The independent variable WEEKS (the number of weeks from the beginning

of the study at each census date) was regressed against the community parameter for the quadrat at each census, starting with the linear term. Successively higher order terms of WEEKS (up to the fourth) were entered stepwise. In order to test whether the combination of the non-linear terms of the polynomial contributed significantly to an explanation of the variation in the data, the linear regression SS was subtracted from the polynomial regression SS and a new F value was calculated. If this F value was significant, the non-linear components were important in explaining variation. It was then concluded that the data showed substantial non-linear fluctuations which might be seasonal or random. An examination of the scattergrams served to indicate which of these two possibilities was most probable. Two of the 12 quadrats were chosen as being representative of those in Curaçao. The scattergrams of the four community parameters for these quadrats are presented in the results for illustrative purposes.

The regression analysis of N_0 (Tables 12-14) revealed that in all quadrats the linear regression was highly significant. The polynomial was significant in most of the quadrats but the F values were generally much lower with only five values attaining the 0.01 significance level. This indicates a strong linear trend in species richness during the study with some seasonal or random fluctuations superimposed (Figs. 13 and 14). An initial rapid increase in species richness occurred in most quadrats owing to the detection of new species with repeated visual sampling. The values generally levelled off

TABLE 12 - Analysis of N_0 against time at transect I (Curaçao)
by quartic polynomial and linear regression (N=36). Poly-
nomial entry is composed of the 3 non-linear terms.

Quadrat	Source of variation	df	SS	MS	F
I-10	polynomial terms	3	191.71	63.90	22.34***
	linear	1	90.46	90.46	10.97***
	deviations from quartic	31	88.58	2.86	
I-20	polynomial terms	3	21.57	7.19	3.00*
	linear	1	39.80	39.80	14.12***
	deviations from quartic	31	74.27	2.40	
I-30	polynomial terms	3	4.37	1.46	0.74
	linear	1	49.30	49.30	25.78***
	deviations from quartic	31	60.64	1.96	
I-40	polynomial terms	3	9.66	3.22	1.93
	linear	1	16.80	16.80	9.28**
	deviations from quartic	31	51.84	1.67	

* $p < 0.05$

** $p < 0.01$

*** $p < 0.001$

TABLE 13 - Analysis of N_0 against time at transect II (Curaçao) by quartic polynomial and linear regression ($N=36$).
Polynomial entry is composed of the 3 non-linear terms.

Quadrat	Source of variation	df	SS	MS	F
II-10	polynomial terms	3	40.17	13.39	3.69*
	linear	1	105.64	105.64	23.54***
	deviations from quartic	31	112.42	3.63	
II-20	polynomial terms	3	39.75	13.25	5.02**
	linear	1	91.97	91.97	25.70***
	deviations from quartic	31	81.92	2.64	
II-30	polynomial terms	3	35.80	11.93	3.81*
	linear	1	75.80	75.80	19.38***
	deviations from quartic	31	97.15	3.13	
II-40	polynomial terms	3	34.99	11.66	4.38*
	linear	1	74.80	74.80	21.66***
	deviations from quartic	31	82.44	2.66	

* $p < 0.05$

** $p < 0.01$

*** $p < 0.001$

TABLE 14 - Analysis of N_0 against time at transect III (Curaçao) by quartic polynomial and linear regression (N=36).
Polynomial entry is composed of the 3 non-linear terms.

Quadrat	Source of variation	df	SS	MS	F
III-10	polynomial terms	3	58.09	19.36	3.86*
	linear	1	96.23	96.23	15.31***
	deviations from quartic	31	155.56	5.02	
III-20	polynomial terms	3	83.89	27.96	6.38**
	linear	1	407.32	407.32	63.04***
	deviations from quartic	31	135.79	4.38	
III-30	polynomial terms	3	83.55	27.85	6.54**
	linear	1	258.05	258.05	40.70***
	deviations from quartic	31	132.04	4.26	
III-40	polynomial terms	3	70.56	23.52	10.23**
	linear	1	67.63	67.63	16.19***
	deviations from quartic	31	71.44	2.30	

* $p < 0.05$

** $p < 0.01$

*** $p < 0.001$

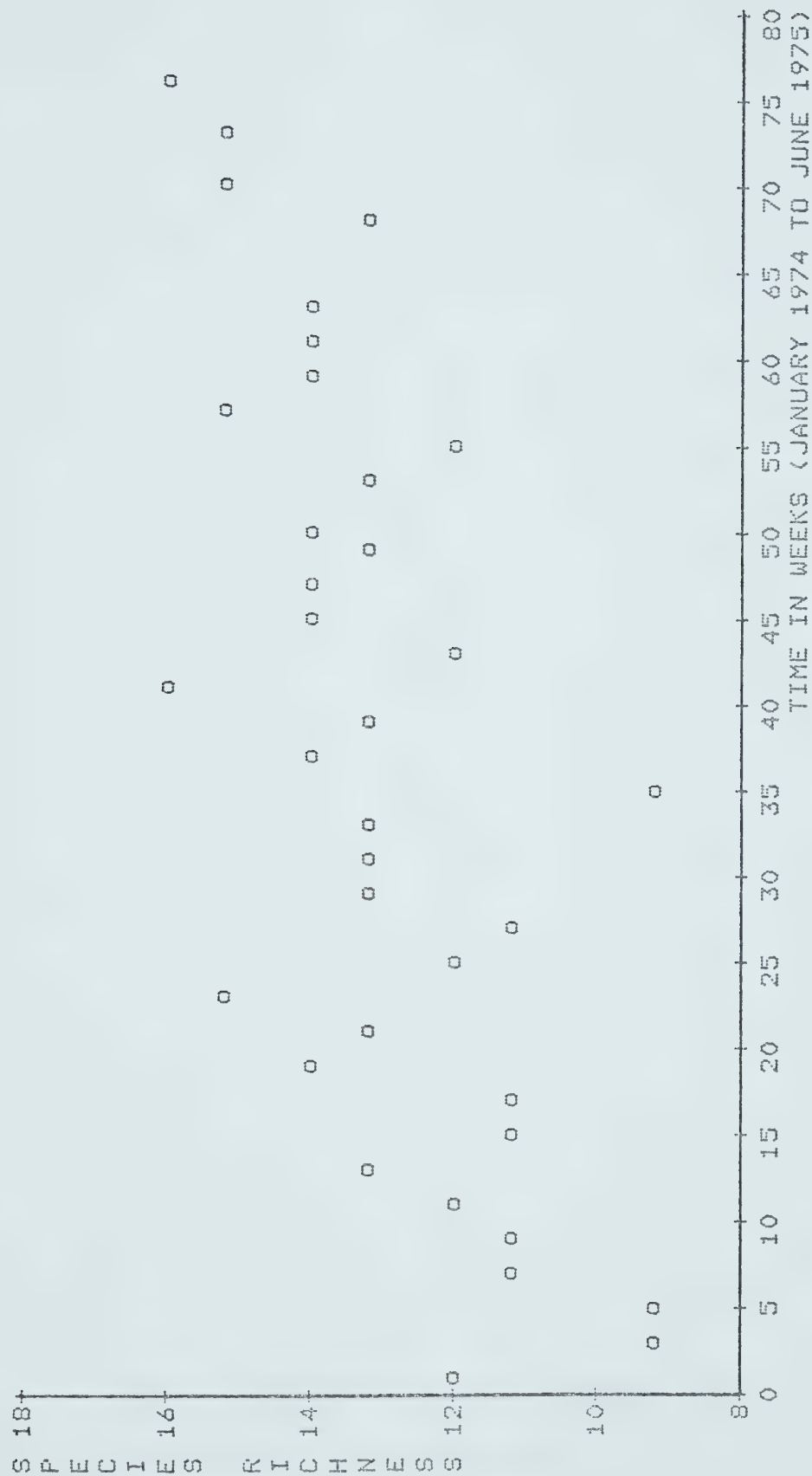


FIG. 13 - Scattergram of species richness (N_0) against time in quadrat I-30.

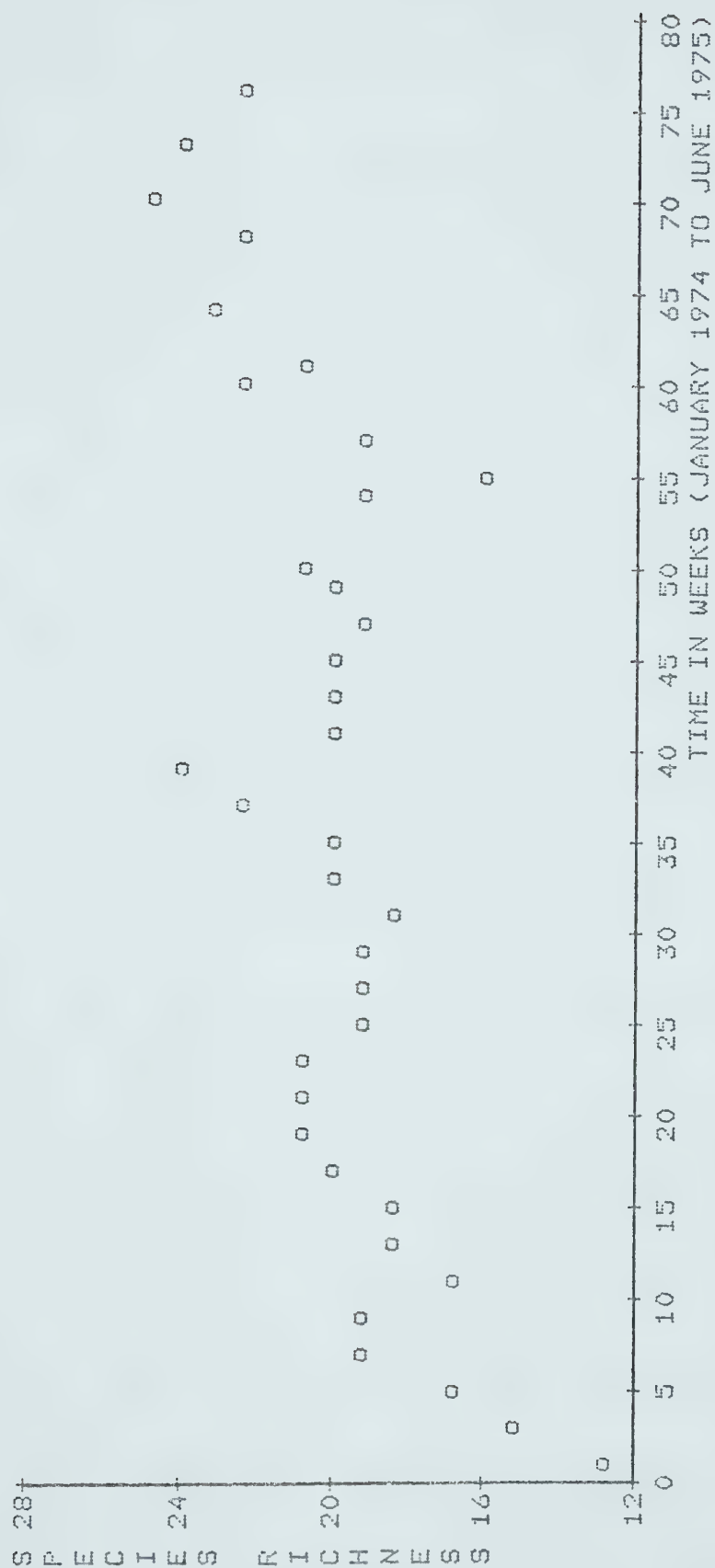


FIG. 14 - Scattergram of species richness (N_0) against time in quadrat II-20.

once most of the species present had been detected. This is a partial explanation of the positive slopes of the regressions with species richness.

The scattergrams of NCP showed large fluctuations in the abundance of individuals, which appeared to be mainly seasonal. In every quadrat but one, the polynomial was highly significant (0.001 level)(Tables 15-17). The linear regression was also significant in a number of quadrats. As there was an obvious cyclical component in the data, another analysis was made. The NCP values were transformed to a sine function ($y = a + b \sin x$) and a simple linear regression performed with WEEKS. None of these regressions was significant, probably owing to the period and amplitude restrictions of the unmodified sine function. The results of the polynomial regression analysis confirm what is evident from the scattergrams (Figs.15,16), that there is a marked seasonal change in the abundance of individuals.

The close correspondence between the scattergrams of NCP and water temperature suggested that there was a relationship between the two variables. Correlation coefficients of NCP with water temperature (for the appropriate depth) produced highly significant values in every quadrat (Table 18). Correlations of N_0 with water temperature also produced many significant values, whereas N_1 and $E_{2.1}$ were generally poorly correlated (Table 18).

Diversity (N_1) showed few systematic fluctuations in most quadrats. In five of the quadrats, the linear regression

TABLE 15 - Analysis of NCP against time at transect I (Curaçao)
by quartic polynomial and linear regression (N=36). Poly-
nomial entry is the combination of the 3 non-linear terms.

Quadrat	Source of Variation	df	SS	MS	F
I-10	polynomial terms	3	23,469.13	7,823.04	8.58***
	linear	1	3,672.91	3,672.91	2.41
	deviations from quartic	31	28,271.19	911.97	
I-20	polynomial terms	3	19,739.83	6,579.94	15.94***
	linear	1	10,937.32	10,937.32	11.43***
	deviations from quartic	31	12,795.41	412.76	
I-30	polynomial terms	3	5,288.14	1,762.71	12.89***
	linear	1	5,484.49	5,484.49	19.57***
	deviations from quartic	31	4,239.68	136.76	
I-40	polynomial terms	3	2,007.70	669.23	20.47***
	linear	1	239.69	239.69	2.70
	deviations from quartic	31	1,013.61	32.70	

*** $p < 0.001$

TABLE 16- Analysis of NCP against time at transect II (Curaçao) by quartic polynomial and linear regression (N=36).
Polynomial entry is the combination of the 3 non-linear terms.

Quadrat	Source of variation	df	SS	MS	F
II-10	polynomial terms	3	7,786.84	2,595.61	2.73
	linear	1	3,127.95	3,127.95	2.86
	deviations from quartic	31	29,436.10	949.55	
II-20	polynomial terms	3	11,027.85	3,675.95	13.11***
	linear	1	4,826.67	4,826.67	8.32**
	deviations from quartic	31	8,693.70	280.44	
II-30	polynomial terms	3	8,410.91	2,803.64	18.29***
	linear	1	7,752.06	7,752.06	20.02***
	deviations from quartic	31	4,752.25	153.30	
II-40	polynomial terms	3	3,024.81	1,008.27	18.84***
	linear	1	3,751.98	3,751.98	27.24***
	deviations from quartic	31	1,659.09	53.52	

** $p < 0.01$

*** $p < 0.001$

TABLE 17- Analysis of NCP against time at transect III (Curaçao)
by quartic polynomial and linear regression (N=36). Poly-
nomial entry is the combination of the 3 non-linear terms.

Quadrat	Source of variation	df	SS	MS	F
III-10	polynomial terms	3	7,990.81	2,663.60	10.07***
	linear	1	9,354.80	9,354.80	19.64***
	deviations from quartic	31	8,201.14	264.55	
III-20	polynomial terms	3	18,773.14	6,257.71	15.10***
	linear	1	23,588.46	23,588.46	25.36***
	deviations from quartic	31	12,846.04	414.39	
III-30	polynomial terms	3	2,108.60	702.87	11.01***
	linear	1	4,369.89	4,369.89	36.34***
	deviations from quartic	31	1,979.51	63.86	
III-40	polynomial terms	3	577.06	192.35	6.60***
	linear	1	294.10	294.10	6.75*
	deviations from quartic	31	904.06	29.16	

* $p < 0.05$

*** $p < 0.001$

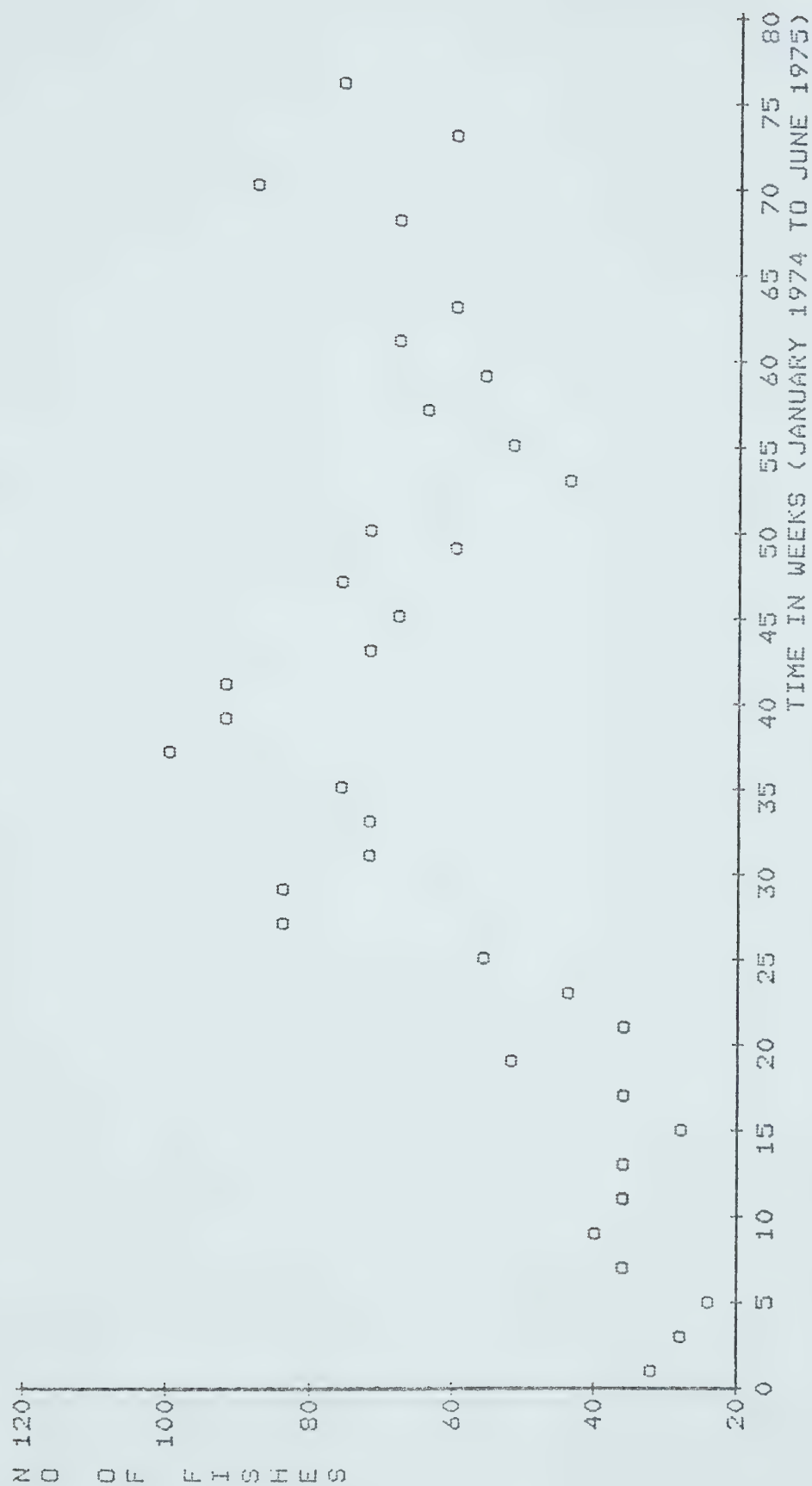


FIG. 15 - Scattergram of number of fishes (NCP) against time in quadrat I-30.

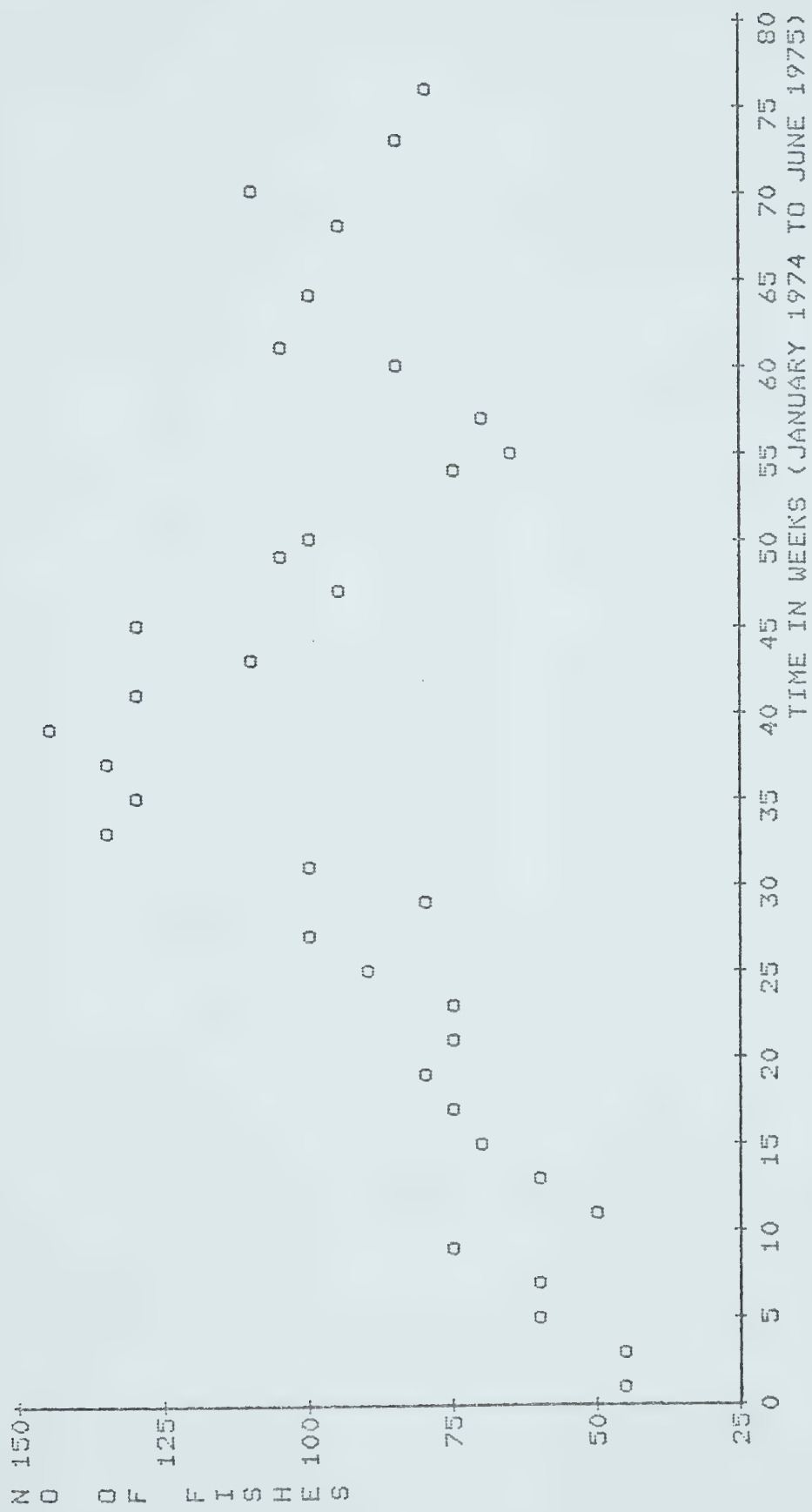


FIG. 16 - Scattergram of number of fishes (NCP) against time in quadrat II-20.

TABLE 18 - Correlation coefficients between four community parameters and water temperature at Curaçao for the period January 1974 to June 1975 (N=36).

Quadrat	Community parameters			
	N_0	NCP	N_1	$E_{2.1}$
I-10	0.693***	0.755***	0.695***	-0.367*
-20	0.614***	0.796***	0.506***	0.501**
-30	0.263	0.727***	-0.271	-0.246
-40	0.366*	0.686***	-0.308	-0.652***
II-10	0.452**	0.609***	0.127	-0.431**
-20	0.289	0.738***	0.179	0.189
-30	0.596***	0.726***	0.185	-0.170
-40	0.477**	0.739***	0.280	0.130
III-10	0.399*	0.652***	0.214	-0.087
-20	0.523**	0.768***	0.320	-0.121
-30	0.412*	0.642***	0.156	-0.292
-40	0.611***	0.555***	0.478**	-0.037

* $p < 0.05$

** $p < 0.01$

*** $p < 0.001$

was highly significant (0.01 level or higher); only two polynomial regressions attained this level (Tables 19-21). Over half of the F values for either linear or polynomial regression were not significant. In those quadrats where most of the total variation was unexplained (no significant F values), fluctuations appeared to be essentially random. With the exception of two quadrats, diversity showed little tendency to fluctuate seasonally. For the most part, temporal changes followed no discernible pattern (Fig. 17), although several quadrats had marked linear trends (Fig. 18).

Evenness ($E_{2.1}$) was generally the most variable of the four parameters, with no consistent trend apparent. Four quadrats had no significant F values, whereas four others had highly significant linear regressions (Tables 22-24). In several of these quadrats, the regressions had negative slopes i.e. the trend was of declining evenness (Fig. 19). In addition, a few quadrats had significant polynomial regressions. Overall the fluctuations in most quadrats provided no evidence of seasonality (Fig. 20).

Discussion

Coral reefs provide a reasonably predictable environment in which seasonal changes are minimal. Smith and Tyler (1972) claim that there is no evidence for "large fluctuations in abundance of reef fishes throughout a yearly cycle", but few studies have monitored the fishes in an area for a sufficiently long period to test the validity of this statement. The temporal analysis of community parameters allows statements

TABLE 19 - Analysis of N_1 against time at transect I (Curaçao)
by quartic polynomial and linear regression (N=36). Poly-
nomial entry is composed of the 3 non-linear terms.

Quadrat	Source of variation	df	SS	MS	F
I-10	polynomial terms	3	53.77	17.92	24.55***
	linear	1	2.26	2.26	1.00
	deviations from quartic	31	22.72	0.73	
I-20	polynomial terms	3	18.84	6.28	2.79
	linear	1	28.64	28.64	11.00**
	deviations from quartic	31	69.62	2.25	
I-30	polynomial terms	3	4.30	1.43	1.04
	linear	1	0.10	0.10	0.07
	deviations from quartic	31	42.82	1.38	
I-40	polynomial terms	3	4.98	1.66	1.27
	linear	1	1.50	1.50	1.11
	deviations from quartic	31	40.75	1.31	

** $p < 0.01$

*** $p < 0.001$

TABLE 20 - Analysis of N_1 against time at transect II (Curaçao) by quartic polynomial and linear regression (N=36).
Polynomial entry is composed of the 3 non-linear terms.

Quadrat	Source of variation	df	SS	MS	F
II-10	polynomial terms	3	7.09	2.36	2.00
	linear	1	36.27	36.27	28.22***
	deviations from quartic	31	36.61	1.18	
II-20	polynomial terms	3	51.82	17.27	3.03*
	linear	1	99.79	99.79	14.85***
	deviations from quartic	31	176.71	5.70	
II-30	polynomial terms	3	2.42	0.81	0.72
	linear	1	17.54	17.54	16.04***
	deviations from quartic	31	34.75	1.12	
II-40	polynomial terms	3	18.82	6.27	1.94
	linear	1	13.22	13.22	3.78
	deviations from quartic	31	100.19	3.23	

* $p < 0.05$

*** $p < 0.001$

TABLE 21 - Analysis of N_1 against time at transect III (Curaçao) by quartic polynomial and linear regression (N=36).

Polynomial entry is composed of the 3 non-linear terms.

Quadrat	Source of variation	df	SS	MS	F
III-10	polynomial terms	3	24.93	8.31	7.77***
	linear	1	5.54	5.54	3.25
	deviations from quartic	31	33.14	1.07	
III-20	polynomial terms	3	23.37	7.79	2.40
	linear	1	71.84	71.84	19.67***
	deviations from quartic	31	100.82	3.25	
III-30	polynomial terms	3	8.45	2.82	0.64
	linear	1	27.22	27.22	6.42*
	deviations from quartic	31	135.63	4.38	
III-40	polynomial terms	3	61.53	20.51	4.21*
	linear	1	35.27	35.27	5.64*
	deviations from quartic	31	150.92	4.87	

* $p < 0.05$

*** $p < 0.001$

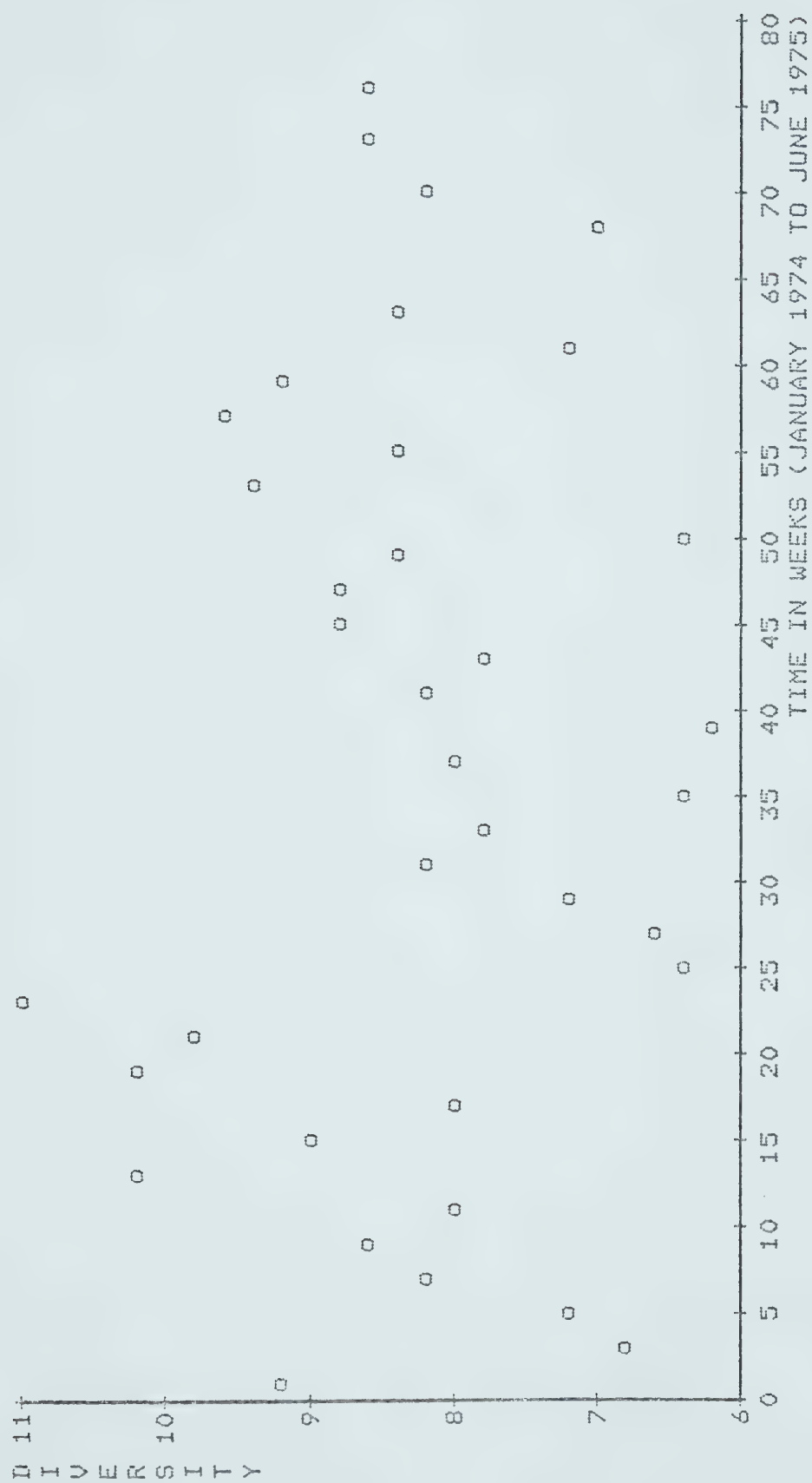


FIG. 17 - Scattergram of diversity (N_1) against time in quadrat I-30.

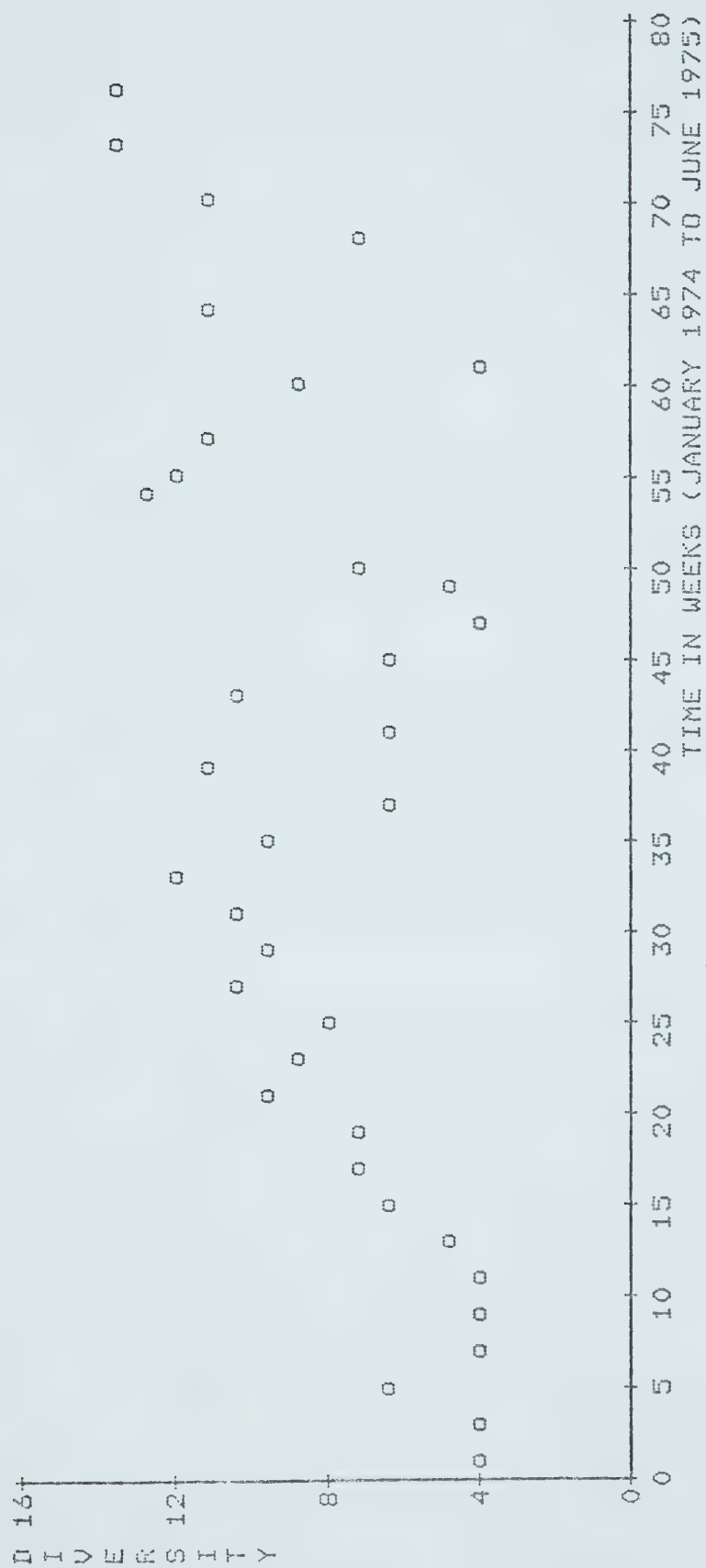


FIG. 18 - Scattergram of diversity (N_1) against time in quadrat II-20.

about the constancy (Oriens 1975) or natural fluctuations of various parameters over the period of the study. It does not provide data on the resilience or stability (Holling 1973) of the communities. These properties can only be assessed if the communities are perturbed in some way and their recovery is monitored. As the communities in this study were purposefully left unperturbed, it is not possible to comment on their resilience or stability. Poisoning of reef areas has shown that fishes rapidly repopulate the vacated area. These areas show complete recovery from the effects of this perturbation within 4-9 months (Smith 1973). Sale and Dybdahl (1975) have shown similar recovery periods for the fishes removed from experimental coral habitats. Both of these studies suggest that reef fish communities are quite stable when subjected to this kind of perturbation. Different forms of perturbation, biological or physical, might yield different results.

An assessment of unperturbed communities provides insight into the natural fluctuations of its various parameters. Individual parameters may be examined for evidence of seasonal or other systematic trends. N_0 appeared to show little seasonal change. There was a strong linear trend in most of the quadrats with some random fluctuations. Many of these fluctuations were undoubtedly caused by visual sampling variability. Chance recruitment of species unsuited to the habitat, which subsequently departed or were removed by predators, may have also caused fluctuations. Immigration and emigration

TABLE 22 - Analysis of $E_{2.1}$ against time at transect I (Curaçao) by quartic polynomial and linear regression (N=36).
Polynomial entry is composed of the 3 non-linear terms.

Quadrat	Source of variation	df	SS	MS	F
I-10	polynomial terms	3	0.009	0.003	3.00*
	linear	1	0.047	0.047	30.57***
	deviations from quartic	31	0.043	0.001	
I-20	polynomial terms	3	0.038	0.013	3.17*
	linear	1	0.013	0.013	2.75
	deviations from quartic	31	0.129	0.004	
I-30	polynomial terms	3	0.007	0.002	1.17
	linear	1	0.042	0.042	18.52***
	deviations from quartic	31	0.071	0.002	
I-40	polynomial terms	3	0.051	0.017	5.67**
	linear	1	0.027	0.027	5.72*
	deviations from quartic	31	0.106	0.003	

* $p < 0.05$

** $p < 0.01$

*** $p < 0.001$

TABLE 23 - Analysis of $E_{2,1}$ against time at transect II (Curaçao) by quartic polynomial and linear regression (N=36).

Polynomial entry is composed of the 3 non-linear terms.

Quadrat	Source of variation	df	SS	MS	F
II-10	polynomial terms	3	0.005	0.002	1.67
	linear	1	0.020	0.020	13.32***
	deviations from quartic	31	0.046	0.001	
II-20	polynomial terms	3	0.043	0.014	1.79
	linear	1	0.021	0.021	2.62
	deviations from quartic	31	0.235	0.008	
II-30	polynomial terms	3	0.011	0.004	0.92
	linear	1	0.006	0.006	1.52
	deviations from quartic	31	0.132	0.004	
II-40	polynomial terms	3	0.023	0.008	1.92
	linear	1	0.004	0.004	0.86
	deviations from quartic	31	0.129	0.004	

*** $p < 0.001$

TABLE 24 - Analysis of $E_{2.1}$ against time at transect III (Curaçao) by quartic polynomial and linear regression (N=36).

Polynomial entry is composed of the 3 non-linear terms.

Quadrat	Source of variation	df	SS	MS	F
III-10	polynomial terms	3	0.007	0.002	2.33
	linear	1	0.012	0.012	11.62***
	deviations from quartic	31	0.028	0.001	
III-20	polynomial terms	3	0.044	0.015	7.25**
	linear	1	0.001	0.001	0.14
	deviations from quartic	31	0.068	0.002	
III-30	polynomial terms	3	0.109	0.036	5.19**
	linear	1	0.013	0.013	1.44
	deviations from quartic	31	0.205	0.007	
III-40	polynomial terms	3	0.079	0.026	2.19
	linear	1	0.007	0.007	0.53
	deviations from quartic	31	0.377	0.012	

** $p < 0.01$

*** $p < 0.001$

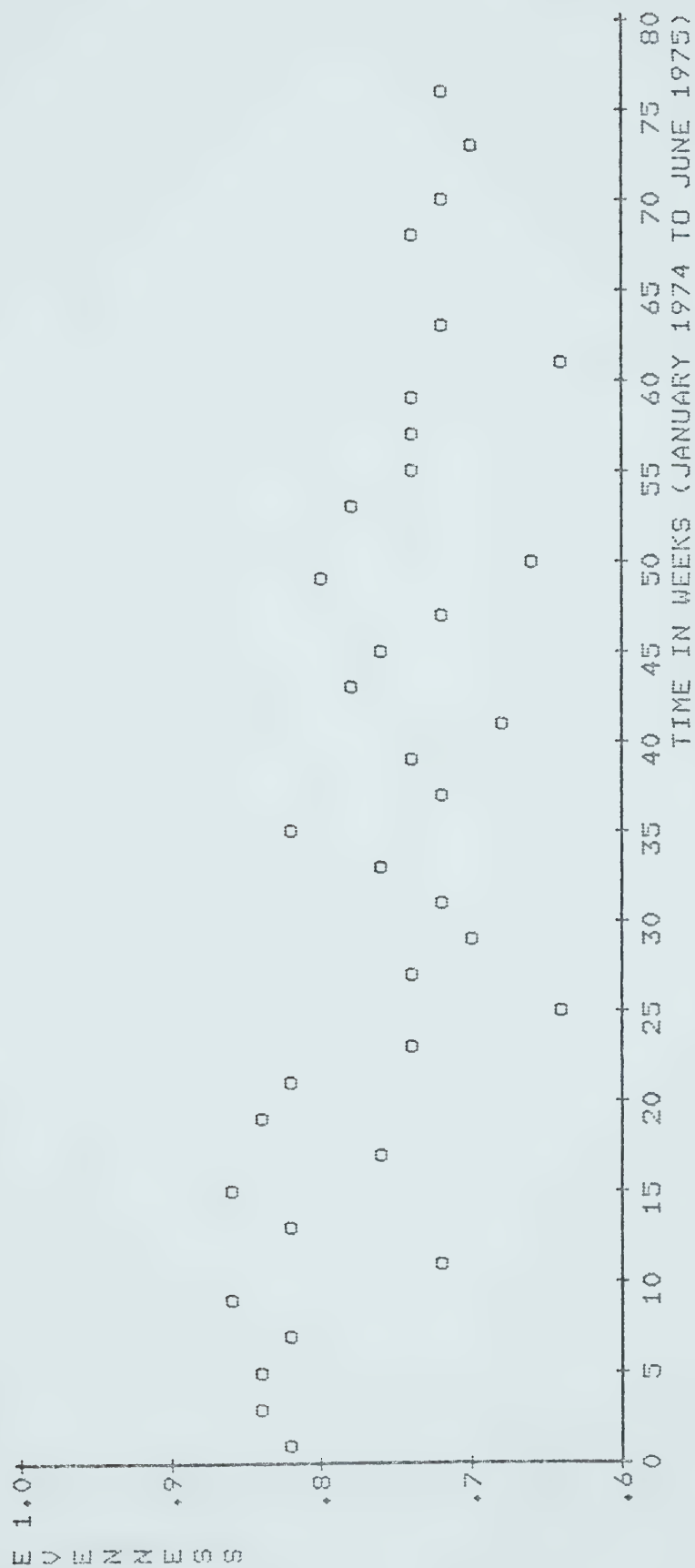


FIG. 19 - Scattergram of evenness ($E_{2.1}$) against time in quadrat I-30.

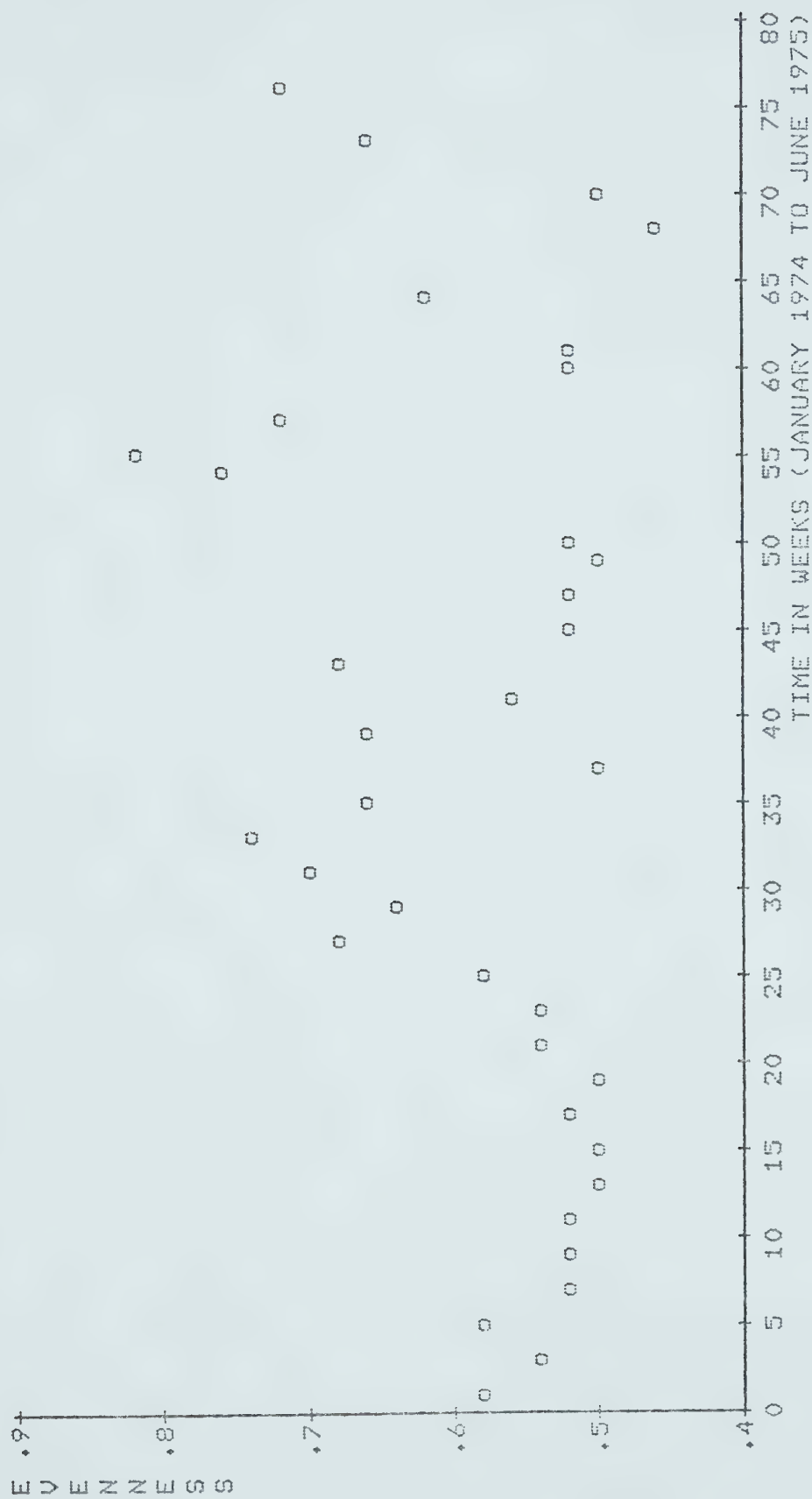


FIG. 20 - Scattergram of evenness ($E_{2.1}$) against time in quadrat II-20.

were unlikely to have been important, owing to the concentration on resident species.

Both N_1 and $E_{2.1}$ were mainly random in their fluctuations, although significant linear trends were apparent in some quadrats. These measures are strongly affected by changes in the relative abundance of component species. Chance recruitment adds individuals and species throughout the year and predation unpredictably removes them, thus constantly changing the relative abundance of species. These two factors, acting together, will probably cause continuous and largely random variations in both diversity and evenness over an 18 month period. They may however, show cyclic stability (Oriens 1975), i.e. they may oscillate within a given range of values, over longer periods. Thomson and Lehner (1976) found that graphs of both diversity (H) and evenness (J) in an intertidal fish community produced nearly flat linear regressions based on collections over a seven year period. However, their diversity measure, H , is not the exponentiated form (e^H) used in the present study; thus the fluctuations of H with time will appear to be of smaller magnitude. Evenness may be similarly influenced owing to the inclusion of H in the formula for evenness ($J = H/H_{\max}$).

The temporal pattern of NCP appeared to be markedly seasonal. The number of individuals gradually increased from January 1974 to a peak in September and then decreased until February-March 1975. Numbers increased again until June of that year when the study ended. This pattern was consistently

found in almost every quadrat. The data on the individual recruitment patterns of the species in the communities (see Figs. 8-12) suggest an explanation for the observed pattern in NCP. Most of the species had two peaks in recruitment during the year. The autumn peak was generally the larger of the two. The absence of a discernible peak in most species in the spring of 1974 has already been discussed. This is reflected in the scattergrams where only a few quadrats show any evidence of a spring peak in 1974 and these peaks are minor. If most of the species in a community had recruitment peaks at the same time of the year, the effect would be additive, causing a marked influx of individuals such as that seen in the fall of 1974. The recruits of several gobiid species had a pronounced effect on NCP, owing to their abundance in the communities. The steady increase in NCP to a peak in September occurred presumably because the overall recruitment rate was sufficiently high that individuals were being added to the community faster than predation was removing them. As the recruitment rate declined in the autumn, predation "cropped" more individuals than were being added and NCP decreased.

The high correlation between NCP and water temperature is suggestive of an indirect causal relationship as temperature is one of the factors most probably regulating spawning periodicity on an annual basis in the tropics (Pearse 1974). Thomson and Lehner (1976) found a highly significant correlation between water temperature and number of individual fishes

in a Gulf of California intertidal community. They attributed the seasonal increase in numbers to recruitment. Monthly (lunar?) cycles may be important in the short term spawning periodicity of reef fishes. Although I do not discount photoperiod, I believe it is less important. At any rate, maximum photoperiod will be out of phase with maximum water temperature. The annual variation in photoperiod at Curaçao is only about 85 minutes (Nautical almanac 1975). As light is rapidly attenuated with depth, the light intensity at 40 m is only 15-20% of that at the surface (Ott 1975). Annual variations in light at the greater depths would be of a lower range and intensity, thus limiting its potential use as a synchronizing factor. De Vlaming (1972) has reviewed the literature on the environmental control of teleost reproductive cycles. A paucity of information on tropical species is evident.

Munro et al. (1973) have proposed that the major spawning season of many reef fish species in Jamaica is correlated with water temperature. They suggested that annual temperature variations determined the periodicity and proportion of spawning fishes and that maximum spawning occurred during the period of minimum water temperature (March-April). Despite the fact that the annual temperature range is only about 3°C ($26.5 - 29.5^{\circ}\text{C}$) in Jamaica, it appears that this variation is sufficiently large for the regulation of fish reproductive cycles. The water temperature range in Curaçao is also about 3°C , with a minimum in the spring; thus the proximate factors

are similar at the two islands. The predictability of the environment probably allows the entrainment of reproduction to this environmental variable despite its small range. Studies of the effect of water temperature and photoperiod on reproduction in tropical reef fishes would do much to clarify the relative influence of these two environmental variables.

The adaptive value of different spawning seasons in the tropics is not well understood, nor is the influence of environmental factors which presumably regulate these cycles. One possibility is that spawning peaks at different times of the year, in closely related species, may serve to reduce competition for space by young juveniles (Smith and Tyler 1972). Several different annual breeding patterns have been observed in tropical echinoderms (Pearse 1974) and further investigations of spawning patterns in reef fishes may provide similar evidence. I suggest that a study of the spawning patterns in a territorial pomacentrid guild, where all members may use resources in a similar way, would be an excellent starting point.

SPATIAL ASPECTS OF COMMUNITIES

Space utilization

In the diverse fish communities found on coral reefs, space has been said to be the most important limiting resource (Smith and Tyler 1972). The species richness of such communities suggests a high degree of species packing and hence the partitioning of resources in many ways. Smith and Tyler (1972) list what they consider to be the six essential aspects of space sharing: 1. hunting and feeding areas, 2. shelter sites, 3. activity cycles, 4. symbiotic relationships, 5. seasonal cycles in reproduction and in the use of space by juveniles, and 6. territoriality. I have concentrated on two of these aspects, the nature and occupancy of shelter sites, and territoriality, in an attempt to elucidate some elements of space resource sharing. Species living in sponges, an example of a symbiotic relationship, were included in the shelter site analysis. Long term field observations (18 months) provided the opportunity to keep a record of which sites in each quadrat were occupied, and by what species. This was accomplished by the use of accurate maps (derived from photographs) of each quadrat and the careful recording of the location of individuals during each census. Two other aspects of space sharing, seasonal cycles in reproduction and activity patterns, have been discussed in previous sections.

It was apparent from many hours of field observation that most species utilize particular kinds of space, but it is difficult to characterize these kinds of space in more

than subjective terms. Six kinds of space or sites were recognized: 1. territories, 2. home ranges, 3. simple ledges, 4. crevices and caves in the reef infrastructure, 5. tube-worm (and similar) holes and 6. sponges. This division is based mainly on association but is dictated largely by the behaviour and movements of the species. A total of 25 species were included in the spatial analysis (Table 25) and the use of each of the six kinds of sites was monitored in each quadrat. Most of the species were fairly sedentary or diurnally inactive; this facilitated visual censusing. Only those sites which were occupied for more than 10% of the study (four or more censuses) in Curaçao were included.

The data allowed the determination of three aspects of the use of space: a) constancy - the percentage of time that a given site was occupied by a species over an extended period (68 weeks), a measure of space utilization, b) consistency - the percentage of time that a site was occupied by a species from its first recorded occurrence at the site, until the end of the study and c) time span - the estimated period of occupancy of each site in weeks.

An analysis showed that few new species were recorded in any of the quadrats following the first four censuses. The species which did occur after this time were relatively rare. This indicates that most of the species which were present at the time, and which could be visually sampled, were detected within four sampling periods. In order to establish a common base for comparisons of all species, the

TABLE 25 - List of the six kinds of sites considered in the spatial analysis and the 25 species associated with them.

Site code	Site	Species
1.	territory	<u>Eupomacentrus dieneae</u> <u>E. partitus</u> <u>E. planifrons</u>
2.	home range	<u>Amblycirrhitus pinos</u> <u>Centropyge argi</u> <u>Enneanectes atrovirens</u> <u>Micrognathus ensenadae</u>
3.	ledge	<u>Apogon townsendi</u> <u>Gramma loreto</u> <u>Myripristis jacobus</u> <u>Priacanthus cruentatus</u> <u>Quisquilius hipoliti</u>
4.	reef infrastructure (crevices, caves)	<u>Apogon lachneri</u> <u>A. phenax</u> <u>Equetus punctatus</u> <u>Holocentrus marianus</u> <u>Liopropoma carmabi</u> <u>L. mowbrayi</u> <u>L. rubre</u> <u>Lipogramma trilineata</u> <u>Plectrypops retrospinis</u>
5.	worm-hole	<u>Acanthemblemaria spinosa</u> <u>Emblemaria bahamensis</u>
6.	sponge	<u>Gobiosoma horsti</u> <u>Starksia hassi</u>

constancy of space utilization was calculated for the last 32 censuses (68 weeks) of the study i.e. for the period following the initial four censuses.

The first occurrence of a species at a site was marked on a permanent map of each quadrat. All subsequent occurrences during censuses were noted and tentative "departure" dates were assigned when an individual was missing. These were amended if, what was thought to be, the same individual was subsequently present during a later census. When estimating periods of occupancy, it was often difficult to determine the exact "departure" dates of many of the smaller species; in these cases, the minimum period was used. This was the time span that the individual could have been present assuming consecutive census occurrences. The data on space utilization in each quadrat, ordered by transect, may be found in Appendix A. A summary of the data for each transect is presented in Tables 26-28.

Major differences were apparent in the constancy and consistency of the use of the six kinds of sites. The three territorial pomacentrid species showed the most constant use of space along all three transects. A total of 13 territories of Eupomacentrus planifrons were monitored and eight of these were continuously occupied for the entire study. The remaining territories were sites where individuals had disappeared or where recruits had moved in to establish a territory. The territories of large, mature fish were occupied, by what I am confident were the same individuals, for periods

TABLE 26 - Space utilization by resident species along transect I. The values given are mean \pm SD (range). For complete species names and explanation of site code, see Table 25.

Site code	Species	No. of sites/ quadrat				Constancy (%)	Consistency (%)	Time span (weeks)
		10m	20m	30m	40m			
1.	<u>E. partitus</u>	-	-	2	-	92.5 \pm 6.4 (88- 97)	88.5 \pm 7.8 (83- 94)	72.0 \pm 5.7 (68-76)
	<u>E. planifrons</u>	-	4	-	-	78.0 \pm 25.4 (56-100)	98.8 \pm 2.5 (95-100)	60.5 \pm 23.7 (39-81)
2.	<u>A. pines</u>	4	-	-	-	44.8 \pm 29.4 (25- 88)	43.5 \pm 23.2 (28- 78)	31.8 \pm 23.3 (15-65)
	<u>C. arci</u>	1	-	-	-	75.0	67.0	76
	<u>E. atrorus</u>	-	1	-	-	16.0	24.0	10
3.	<u>A. townsendi</u>	1	-	-	-	72.0	85.0	57
	<u>C. loreto</u>	-	1	6	3	36.0 \pm 17.8 (13- 69)	42.0 \pm 15.1 (25-100)	20.7 \pm 13.5 (6-48)
	<u>C. hicoliti</u>	5	19	16	9	31.6 \pm 12.5 (13- 63)	49.0 \pm 19.6 (18- 94)	20.1 \pm 8.0 (8-40)
4.	<u>A. phenax</u>	-	-	2	1	30.3 \pm 14.7 (19- 47)	47.3 \pm 4.2 (44- 52)	32.0 \pm 16.4 (14-46)
	<u>H. marianus</u>	-	3	-	-	48.0 \pm 45.1 (19-100)	56.0 \pm 35.4 (24- 94)	38.7 \pm 32.6 (16-76)
	<u>L. carnabi</u>	-	-	1	-	13.0	16.0	24
	<u>L. mowbrayi</u>	-	-	-	1	19.0	33.0	22
	<u>L. rubre</u>	-	3	-	-	22.0 \pm 10.8 (13- 34)	46.0 \pm 15.0 (31- 61)	22.7 \pm 15.6 (8-39)
	<u>L. trilineata</u>	-	3	2	-	22.0 \pm 6.0 (16- 28)	33.0 \pm 13.9 (21- 53)	19.6 \pm 11.6 (10-35)
	<u>P. retrospinis</u>	-	2	-	-	33.0 \pm 11.3 (25- 41)	43.5 \pm 9.2 (37- 50)	39.5 \pm 6.4 (35-44)
5.	<u>A. spinosa</u>	1	-	-	-	16.0	14.0	8
	<u>E. bahamensis</u>	2	-	-	-	30.0 \pm 24.0 (13- 47)	36.5 \pm 30.4 (16- 58)	17.5 \pm 16.3 (6-29)
6.	<u>S. hassi</u>	1	-	-	-	25.0	80.0	23

TABLE 27 - Space utilization by resident species along transect II. The values given are mean \pm SD (range). For complete species names and explanation of site code, see Table 25.

Site code	Species	No. of sites/ quadrat				Constancy (%)	Consistency (%)	Time span (weeks)
		10m	20m	30m	40m			
1.	<u>E. dienciaeus</u>	3	-	-	-	83.3 \pm 28.9 (50-100)	100.0	65.0 \pm 26.0 (35-80)
	<u>E. partitus</u>	-	4	3	-	71.3 \pm 22.0 (44-100)	78.3 \pm 20.8 (53-100)	54.3 \pm 17.3 (33-80)
	<u>E. planifrons</u>	1	2	-	-	61.7 \pm 42.5 (16-100)	77.3 \pm 20.3 (61-100)	45.7 \pm 27.8 (16-71)
2.	<u>A. pinos</u>	6	-	-	-	53.3 \pm 25.7 (22- 88)	58.0 \pm 17.5 (34- 78)	47.5 \pm 16.7 (24-68)
	<u>E. atrorox</u>	-	3	-	-	39.7 \pm 18.6 (22- 59)	43.7 \pm 16.6 (26- 59)	42.7 \pm 28.0 (12-67)
3.	<u>A. townsendi</u>	-	-	-	1	22.0	27.0	14
	<u>G. loreto</u>	-	10	15	15	39.1 \pm 19.7 (13-100)	60.6 \pm 26.5 (18-100)	30.3 \pm 17.5 (6-76)
4.	<u>A. hipoliti</u>	8	13	20	16	33.0 \pm 19.6 (13- 94)	45.5 \pm 21.9 (16- 96)	21.2 \pm 12.7 (8-60)
	<u>A. phenax</u>	-	4	4	-	25.6 \pm 15.4 (13- 53)	47.9 \pm 25.8 (21-100)	21.8 \pm 17.7 (8-58)
	<u>H. marianus</u>	-	2	-	1	61.3 \pm 35.3 (31-100)	56.3 \pm 30.7 (28- 89)	63.3 \pm 11.7 (53-76)
	<u>L. mowbrayi</u>	-	-	-	1	13.0	25.0	13
	<u>L. rubre</u>	-	8	4	-	36.4 \pm 20.4 (13- 72)	41.2 \pm 25.6 (17-100)	34.8 \pm 20.6 (8-68)
	<u>L. trilineata</u>	-	4	3	1	27.6 \pm 23.9 (13- 78)	35.1 \pm 20.3 (13- 74)	25.6 \pm 22.7 (8-68)
5.	<u>P. retrospinis</u>	-	2	-	1	66.7 \pm 44.6 (16-100)	68.3 \pm 32.5 (33- 97)	58.0 \pm 27.0 (27-76)
	<u>A. spinosa</u>	15	-	-	-	33.9 \pm 23.5 (13-100)	49.8 \pm 33.8 (15-100)	21.1 \pm 16.3 (6-67)
6.	<u>E. bahamensis</u>	4	1	-	-	16.6 \pm 3.9 (13- 22)	47.4 \pm 34.3 (15-100)	10.6 \pm 4.2 (6-15)
	<u>G. horsti</u>	1	-	-	-	100.0	100.0	76

TABLE 28 - Space utilization by resident species along transect III. The values given are mean \pm SD (range). For complete species names and explanation of site code, see Table 25.

Site code	Species	No. of sites/ quadrat			Constancy (%)	Consistency (%)	Time span (weeks)
		10m	20m	30m 40m			
1.	<u>E. partitus</u>	-	-	2	42.0 \pm 19.8 (28- 56)	47.5 \pm 3.5 (45- 50)	34.5 \pm 17.7 (22-47)
	<u>E. planifrons</u>	4	2	-	89.7 \pm 25.3 (38-100)	95.8 \pm 10.2 (75-100)	68.8 \pm 17.6 (33-76)
2.	<u>A. pinos</u>	5	-	-	46.2 \pm 27.0 (16- 84)	59.0 \pm 31.7 (19-100)	45.2 \pm 25.8 (10-69)
	<u>E. atrovus</u>	-	1	1	23.5 \pm 2.1 (22- 25)	40.0 \pm 9.9 (33- 47)	38.0 \pm 9.9 (31-45)
3.	<u>M. enseredae</u>	-	1	-	28.0	53.0	32
	<u>A. townsendi</u>	-	8	-	35.5 \pm 18.0 (13- 66)	53.3 \pm 23.6 (17- 88)	34.5 \pm 17.4 (8-51)
	<u>G. loreto</u>	-	4	21	28.9 \pm 16.7 (13- 78)	45.9 \pm 25.1 (18-100)	20.8 \pm 13.4 (6-59)
	<u>M. jacobus</u>	2	1	-	56.3 \pm 36.9 (25- 97)	72.7 \pm 35.9 (32-100)	54.0 \pm 21.5 (33-76)
	<u>P. cruentatus</u>	-	1	1	26.3 \pm 20.6 (13- 50)	52.3 \pm 7.2 (44- 57)	35.3 \pm 35.6 (10-76)
	<u>G. hinoliti</u>	9	18	11	30.9 \pm 14.3 (13- 72)	47.2 \pm 20.4 (17-100)	20.0 \pm 9.3 (8-46)
4.	<u>A. lachneri</u>	-	4	-	35.0 \pm 16.4 (22- 59)	43.8 \pm 19.7 (26- 67)	30.5 \pm 10.2 (16-39)
	<u>A. phenax</u>	-	2	4	22.6 \pm 11.2 (13- 44)	31.9 \pm 6.5 (22- 41)	31.7 \pm 18.4 (8-69)
	<u>E. punctatus</u>	1	-	-	41.0	42.0	46
	<u>H. marianus</u>	1	3	1	51.0 \pm 25.2 (16- 81)	49.6 \pm 21.6 (19- 81)	56.1 \pm 21.7 (25-76)
	<u>E. carmabi</u>	-	-	1	13.0	25.0	20
	<u>L. rubre</u>	-	5	8	24.6 \pm 12.0 (13- 53)	39.3 \pm 16.7 (17- 79)	23.1 \pm 17.2 (8-66)
	<u>L. trilineata</u>	-	4	6	24.5 \pm 16.7 (13- 63)	34.6 \pm 16.2 (21- 77)	20.1 \pm 17.6 (8-56)
	<u>P. retrospinis</u>	-	2	1	63.3 \pm 21.8 (31- 78)	72.0 \pm 8.4 (63- 83)	56.8 \pm 19.5 (28-71)
5.	<u>A. spinosa</u>	33	-	-	55.0 \pm 29.9 (13-100)	72.9 \pm 31.4 (13-100)	36.2 \pm 21.3 (6-69)
	<u>E. bahatensis</u>	3	2	-	25.8 \pm 15.9 (13- 53)	46.0 \pm 35.9 (15-100)	17.0 \pm 14.1 (7-42)
6.	<u>G. horsti</u>	1	-	-	19.0	21.0	52
	<u>E. hassi</u>	1	-	-	38.0	43.0	59

of up to 81 weeks (Table 26). A number of these individuals were identifiable by scars or other distinctive markings. Eupomacentrus dioncaeus was found only in one quadrat (II-10). Two of the three territories were continuously occupied for a period of 80 weeks (Table 27). No attempt was made to monitor the territories of E. partitus in most of the shallower quadrats (10 and 20 m) because they were too numerous and were more difficult to define. However, the number of mature individuals showed only small fluctuations in all of these quadrats throughout the study, suggesting a high degree of constancy in the number, and presumably the use, of these territories. The territories of mature fish in some of the deeper quadrats showed the same constancy of use over long periods as their congeners (Table 27).

Of the four species whose sites were listed as a home range, only one the cirrhitid Amblycirrhitus pinos, was relatively common. It was recorded only at 10 m. The mean values for the three quadrats are remarkably similar (Tables 26-28). The percentages are probably underestimates owing to the difficulty in detecting this species when it is amongst corals. Centropyge argi, a chaetodontid, was found in only one quadrat (I-10). It had a well defined home range and was present for most of the study (Table 26). Enneanectes atrorus, a small cryptically coloured clinid, appeared to move within a small limited area. One site was occupied for 59% of the study (Table 27), but mean values were considerably lower. A syngnathid, Micrognathus ensenadae was found within

the same area (about $5m^2$) of a quadrat for 53% of the time since its first recorded occurrence (Table 28). This uncommon species was sighted in several other quadrats but never consistently.

Three of the species associated with ledges were nocturnally active. Two of these, the holocentrid Myripristis jacobus and the priacanthid Priacanthus cruentatus, are relatively large species and are limited to sites of sufficient size to provide shelter. Both of these species were found at only one transect (III). The former species was very consistent in its occurrence (Table 28), apparently returning to the same location (a 50-75 cm section of a ledge) after nocturnal foraging. P. cruentatus appears to have a larger home range and probably employs several shelter sites, but one site was occupied for 50% of the study over a period spanning 76 weeks (Table 23). The apogonid, Apogon townsendi, showed considerable variability in the constancy of use of space, but once present it was usually quite consistent (Table 28). At several sites, more than one individual of this species was present at the same time.

Two of the other species generally associated with ledges had restricted home ranges. The grammid, Gramma loreto, hovers within about 25 cm of its shelter hole, picking zooplankton. It retreats into its hole under a ledge when disturbed. The gobiid, Quisquilius hipoliti, which may be extremely abundant in some areas, usually rests on its pelvic fins under a ledge and darts out to strike at small planktonic

organisms. For G. loreto mean values for constancy of use along the three transects were similar (Tables 26-28). When the calculations were made with the sites of mature individuals only, all of the means increased to about 50%, indicating a more constant use of space by mature fish than by juveniles or recruits. A total of 147 sites were monitored for Q. hipoliti, the largest sample for any of the species. All three transects have strikingly similar mean values for constancy, consistency and time span (Tables 26 - 28). Because the sample sizes are large, I believe the figures to be a reasonably accurate reflection of these parameters in this species.

There are many species which normally move about or shelter within the reef infrastructure. The characterization of the different uses which are made of this space is difficult owing to the fact that it is usually inaccessible for observation. A cave may be the home range of some of the smaller diurnal species and the shelter site of a nocturnally active species.

Two nocturnal apogonid species, Apogon lachneri and A. phenax, typically prefer different kinds of shelter sites within the reef. The former species is usually found in relatively small, dark caves while the latter is most common in dark, enclosed crevices of small dimensions (10-15 cm). Livingston (1971) noted differences in the microhabitats of the apogonid species he studied in Florida and his description of the microhabitat of A. lachneri is similar to that

given here. This species was uncommon except in one quadrat where it was fairly constant (Table 28), although the sample size is small. The sites used by A. phenax were more numerous and show similar mean values in most comparisons between transects (Tables 26-28).

The holocentrids, Holocentrus marianus and Plectrypops retrospinis, were amongst the species exhibiting the most constant and consistent use of space (Tables 26 - 28). The mean values of these measures for these two species were the highest recorded except for the pomacentrids. Two of the 13 sites of H. marianus had a constancy of 100%, while four of the nine sites of P. retrospinis had constancy values over 75%. As in the apogonids, differences in shelter sites were apparent; H. marianus remained in open caves with some light, while P. retrospinis was usually found in the deeper, darker recesses of the reef.

A single mature sciaenid, Equetus punctatus, occupied a site under an eroded coral head for 41% of the study (Table 28). It apparently had a reasonably large home range and may have used several shelter sites.

Three species in the serranid genus Liopropoma, L. carmabi, L. mowbrayi and L. rubre were invariably observed within the reef infrastructure and rarely ventured into the open. The latter species was observed relatively often, while the former two species were found only at the deeper quadrats (30 and 40 m); they were not common. The detection of these

species on a consistent basis was difficult owing to the labyrinthine nature of the reef; therefore, the percentages are undoubtedly underestimates. The mean constancy values for L. rubre show some variation while consistency is similar (Tables 26 - 28). Of the total of 30 sites which were monitored, 11 were occupied for longer than half of the study (38 weeks), indicating long term use of sites. Both L. carmabi and L. nowbrayi were represented at only two sites each, and neither species was very constant (Tables 26 - 28). They are secretive species which move quickly through the reef infrastructure; thus they are particularly difficult to census. The time spans of occupancy (up to 24 weeks) support the suggestion of underestimation of percentages.

The final species listed in association with the reef infrastructure, the grammid, Lipogramma trilineata, was often found under ledges as well, but it was rarely as visible as Gramma loreto. Only slight disturbances may cause it to dart into its shelter hole. A comparison of the mean values for the transects (Tables 26 - 28), shows only minor differences, suggesting some regularity in the level of censusing by the observers and in the behaviour of the species. Again, the time spans at some sites (up to 68 weeks) suggest underestimates in the percentages.

Two clinid species, Acanthemblemaria spinosa and Emblemaria bahamensis were assigned to the fifth site category. Both species were most often seen in abandoned serpulid tube-worm holes, but may utilize any form of eroded hole provided

it is of the correct dimensions. A. spinosa is generally far more abundant than E. bahamensis. A total of 49 different holes of the former species (all at 10 m) were monitored during the study. The 12 sites of E. bahamensis were located at both 10 and 20 m quadrats. A. spinosa had higher percentages and longer time spans than E. bahamensis (Tables 26 - 28). The low value for A. spinosa at I-10 (Table 26) was due to the disappearance of the lone individual shortly after the study began. Twelve of the A. spinosa sites had constancy values greater than 80%.

The species which are obligate sponge dwellers can be expected to show a high degree of constancy and consistency owing to their very limited home range. Facultative sponge dwellers may be more variable. One species from each group was recorded. The gobiid, Gobiosoma horsti, an obligate species (Tyler and Böhlke 1972) was found in two different species of sponge (Callyspongia sp. and Neofibrularia massa ?). As expected, it was continuously present for the entire study at one site (Table 27). The other site had intermittent occurrences of recruits and juveniles but never any mature individuals. The facultative species, a clinid, Starksia hassi, was found only in Callyspongia sp. The data are from only two sites. One of the sites, occupied for 23 weeks, had a consistency of 80% (Table 26), while the other was less consistent but was occupied over a span of 59 weeks.

Discussion

If it is accepted that space is the resource most limited on coral reefs, then it is reasonable to expect that many species will have evolved behaviour patterns to ensure an adequate amount of living space. Predation pressure appears to be very high on reefs (Hobson 1968, 1973), thus there must be strong selection against species straying too far from cover. As most species require a certain kind of shelter site, the presence and abundance of the requisite shelter will have a strong influence on whether the species is likely to be successful in becoming established in that habitat. The proximity of appropriate feeding or hunting areas to the shelter site will also be important. Predation pressure, the distribution of food resources and the availability of refugia will all influence the size and shape of foraging areas (Covich 1976).

Smith and Tyler (1972) suggested that "if the individual's home site is rigorously guarded and defended against all intruders, this could be an important mechanism for stabilizing the community." There are few data available on the behaviour of most species regarding the defence of a shelter site. However, data on the constancy and consistency of use of specific shelter sites should provide a means for assessing its possible stabilizing influence on the community. If a certain individual consistently uses the same shelter site, this may be accomplished either by active guarding of the site against other individuals, or by passive exclusion

owing to the individual's presence.

Only three of the species considered in the spatial analysis exhibit true territorial behaviour (Brown and Orians 1970); all are species of the pomacentrid genus Eupomacentrus. E. planifrons and E. dieneaeus are benthic feeders while E. partitus is mainly planktivorous. All three species defend a well-defined area rather than a specific hole, but the basis for this defence is more clear in E. planifrons (Myrberg and Thresher 1974), and its congener E. dieneaeus, than in E. partitus (Myrberg 1972). These species show intra- and inter-specific defence; since the territories are virtually constantly occupied, the territory holders must have a very influential effect on the use of space.

The home range of Amblycirrhitis pinos often broadly overlaps with the territories of these pomacentrids, but there seems to be little interaction between them. This overlap of home ranges and territories may be observed at several levels down to the smaller gobies and clinids. This is one of the mechanisms permitting the intensive use of space on coral reefs i.e. there are few exclusive areas. When there is extensive spatial overlap in non-labile species, feeding specializations often tend to reduce competition. This has been demonstrated in bird communities (Cody 1974).

Two of the important nocturnally active families, the holocentrids and apogonids, shelter in the reef during the day, disperse at night to feed, and then return, generally to the same site, at dawn. Obviously, topographic orientation

(Jander 1975) is involved in this return to the site. These species show some of the characteristics of refuging (Hamilton and Watt 1970), but on an individual rather than a group basis. The high constancy values for Holocentrus marianus, Plectrypons retrospinis and Myripristis jacobus indicate that the same shelter sites are used over long periods. These species are among the larger ones included in the study and their consistent presence in the reef infrastructure will influence the space available to other species. I have no evidence of active guarding of sites by any of these species; in fact, in one cave H. marianus, M. jacobus and Equetus punctatus were frequently found together. Individual apogonid sites were occupied for most of the study but mean values were generally lower than those for the holocentrids. This suggests more variable use of space, or return to the same general area after foraging, but not the same site. These observations on holocentrids and apogonids are in general agreement with those of Smith and Tyler (1972).

Two of the species associated with ledges, Gramma loreto and Quisquilius hipoliti, were not as constant as other species but mean values were 30-40%. These species move in small circumscribed areas, but can be very abundant in certain locations, effectively using much of the ledge space available.

The species of Liopropoma have lower constancy values than most of the other species, but these undoubtedly are

underestimates as the same sites were occupied, by what appeared to be the same individuals, for periods of up to 68 weeks. Their home ranges within the reef infrastructure may be as large as the size of the quadrat. Lipogramma trilineata was never observed to move more than about 75 cm from a central shelter hole and the low percentage values are probably due to its secretive nature. The two species which resided in tube-worm holes occupied a microhabitat which requires some morphological specialization; thus it is open to only a few species. Holes were occupied by Acanthemblemaria spinosa for long periods (up to 69 weeks), presumably by the same individuals. When vacated, some holes were re-occupied within a few days by an individual of the same species. Several vacated Emblemaria bahamensis holes were occupied by A. spinosa within two days. This suggests that suitable holes for this species may be in short supply.

Some species have become morphologically specialized to inhabit sponges while others appear to use sponges simply as shelter sites (Tyler and Böhlke 1972). The use of sponges for shelter sites may simply be a means of reducing competition for a limited resource.

Smith and Tyler (1972) have suggested that even if "only a relatively small fraction of the species present" defend their home sites, it would have the effect of providing a stable base population against which the more labile species would need to compete. I believe this argument may be extended to include species exhibiting a high degree of

spatial constancy, without evidence of home site defence. It should be recalled that all sites occupied for four or more censuses were included in the calculation of the mean values (Tables 26 - 28). Therefore, sites only recently occupied near the end of the study, or those which were occupied for only the minimum period before being vacated, tend to decrease the mean values substantially. The stochastic nature of mortality and recruitment are thus partially accounted for in the mean values, but the range indicates that maximum values are often very high. A more intensive study of a few sites, possibly with marked individuals, would do much to amplify these findings.

A survey of the data indicates that the territorial pomacentrids, by virtue of their spatial constancy, will be the most influential group affecting the movements (and feeding) of the more labile species (Low 1971; Vine 1974; Moran and Sale 1977). The holocentrids and apogonids appear to be the two groups most likely to influence the diurnal use of space in the reef infrastructure. This influence will probably not be as direct or overt as that of the territorial pomacentrids, but may be just as significant.

The data presented here support the contention that space may be the most important limiting resource on reefs. Mean values for space utilization are very high in some species; these are generally the larger, longer-lived species. The lower constancy values occur mostly in the smaller, less

conspicuous species which may complete their life cycle in less than one year and thus have a higher turnover rate. The lower constancy values in some of the species are also partially the result of the limitations of visual censusing in a topographically complex environment. The stochastic nature of the recruitment-loss process on the reef will probably limit spatial constancy to values considerably less than 100 % in most species. This should not be taken as evidence that the availability of suitable space is not of fundamental importance to reef fishes.

Space sharing

An aspect of the use of space which is very important is the diurnal-nocturnal sharing of the same shelter sites. This use of space in "shifts" is one of the factors promoting a higher degree of species packing. During the dawn and dusk changeovers, nocturnal and diurnal species change positions in a characteristic sequence (Hobson 1965; Collette and Talbot 1972; Domm and Domm 1973). Diurnal-nocturnal observations in the same quadrats provide information on the extent of movement (home ranges) of species and on the sharing of the same shelter site by different species. The non-labile species remain within the same area both day and night (Table 29). The species involved in the nocturnal phase of space sharing (Table 30) are most often diurnal planktivores. These species commonly form schools which feed above the substrate. At dusk, these schools break up and the individuals seek shelter either singly or in small groups.

The two most abundant species sheltering at night were Clepticus parrai and Chromis multilineatus. The former species consistently used the same sites (Table 30), which were all occupied by lone individuals. Collette and Talbot (1972) found the same crevice occupied by Clepticus parrai on several occasions on their study reef. Chromis multilineatus was too abundant at the shallower depths to monitor individual sites, but it appeared to be less precise in the use of space. As many as three or four individuals were found together under the same ledge. This species was usually more conspicuous

TABLE 29 - Diurnal and nocturnal space utilization of sites by species. Only the sites included in the spatial analysis of each quadrat are considered.

Quadrat	No. of sites	Sites	Species
I-10	1	home range	<u>Amblycirrhitus pinos</u>
	1	worm hole	<u>Emblemaria bahamensis</u>
I-20	1	territory	<u>Eupomacentrus planifrons</u>
I-30	2	cave*	<u>Apogon phenax</u>
II-10	1	territory	<u>Eupomacentrus dienciaeus</u>
	1	territory	<u>Eupomacentrus planifrons</u>
	1	home range	<u>Amblycirrhitus pinos</u>
	2	worm hole	<u>Acanthemblemaria spinosa</u>
	1	sponge	<u>Gobiosoma horsti</u>
II-20	1	cave	<u>Plectrypops retrospinis</u>
III-10	1	territory	<u>Eupomacentrus planifrons</u>
	1	home range	<u>Amblycirrhitus pinos</u>
	18	worm hole	<u>Acanthemblemaria spinosa</u>
	1	worm hole	<u>Emblemaria bahamensis</u>

* within 20 cm of the entrance

TABLE 30 - Diurnal-nocturnal space sharing of the same shelter sites. Only the sites included in the spatial analysis are considered. See Table 1 for generic names.

Quadrat	Site(s)	Diurnally occupied by	Nocturnally occupied by
I-10	sponge	<u>S. hassi</u>	<u>E. partitus</u>
I-30	cave	<u>L. carmabi</u>	<u>C. cyaneus</u>
I-40	ledge	<u>Q. hipoliti</u>	<u>C. parrai</u>
II-40	ledge	<u>P. retrospinis</u>	<u>C. parrai</u>
III-10	cave	<u>E. punctatus</u>	<u>C. cyaneus</u>
		<u>H. marianus</u>	
	sponge	<u>S. hassi</u>	<u>T. bifasciatum</u>
III-20	ledge	<u>P. retrospinis</u>	<u>C. parrai</u>
	ledge	<u>L. trilineata</u>	<u>C. parrai</u>
		<u>P. retrospinis</u>	
	ledge	<u>L. rubre</u>	<u>C. parrai</u>
		<u>P. retrospinis</u>	
	ledge	<u>G. loreto</u>	<u>C. parrai</u>
		<u>L. rubre</u>	
	ledge	<u>H. marianus</u>	<u>C. cyaneus</u>
	ledge	<u>A. townsendi</u>	<u>C. cyaneus</u>
	cave	<u>A. townsendi</u>	<u>C. parrai</u>
III-30	ledge	<u>L. trilineata</u>	<u>C. cyaneus</u>
	cave	<u>L. rubre</u>	<u>A. lachneri</u>
	ledge	<u>G. loreto</u>	<u>C. parrai</u>
			<u>P. retrospinis</u>
III-40	ledge	<u>H. marianus</u>	<u>C. parrai</u>
	ledge	<u>L. rubre</u>	<u>C. cyaneus</u>
		<u>P. retrospinis</u>	<u>C. insolatus</u>

than its congener, Chromis cyaneus, which consistently used the same sites (Table 30). Collette and Talbot (1972) noted a similar difference between these two species, with C. cyaneus being found deeper in crevices. Starksia hessi was not observed in its sponge (Callyspongia sp.) at night (Table 30). It may have left to forage outside the sponge or have been deeper inside so that it was not visible. The two species using these sponges at night, Eupomacentrus partitus and Thalassoma bifasciatum, were present at every nocturnal census. Smith and Tyler (1972) also recorded the latter species in a sponge of the same genus at night. The nocturnal species, Apogon lachneri and Plectrypops retrospinis, are among those species that feed close to the substrate; their occurrence at the two sites in III-30 (Table 30) may not be a true case of space sharing.

RELATIONSHIP BETWEEN FISH PARAMETERS AND SUBSTRATE VARIABLES

Analysis of substrate variables

The values of three substrate variables - substrate rugosity (SR), vertical relief (VR) and coral species richness (CS) were determined for each quadrat in the study. These data are summarized in Table 31. The largest SR values in Curaçao were generally found at 20 m. The 10 m values were highly variable while the 30 and 40 m values showed a progressive decrease with depth. The SR and VR for each quadrat were highly correlated ($r=0.848$, $p < 0.001$) and hence the vertical relief pattern with depth closely parallels that of the SR. Photographs of each quadrat may be found in Appendix B.

In Bonaire, the pattern for the single transect showed a relatively large SR at 10 m and the values decreased with depth. Again, SR and VR were highly correlated ($r = 0.991$, $p < 0.01$). It is difficult to attribute much significance to a single pattern; however, survey dives at eight different locations along the leeward coast indicated that vertical relief was usually greater at 10 m in Bonaire than at Curaçao. Coral species richness (CS) at both islands was greatest at 10 or 20 m and declined with depth (Table 31).

Individual SR values ranged from 1.10 in areas of sandy rubble to 4.60 in topographically complex areas with large vertical relief and small caves. In order to determine if the ledges projecting outward from the reef slope had an influence on the SR of a quadrat, the means of the measure-

TABLE 31 - Values of three substrate variables, substrate rugosity (SR), vertical relief (VR) and coral species richness (CS) from three transects (I, II, III) at Curaçao and one transect (IV) at Bonaire. The values for SR and VR are means \pm SD.

Depth (m)	Variable	Transects			
		I	II	III	IV
10	SR	1.28 \pm 0.16	1.65 \pm 0.35	2.06 \pm 0.42	3.62 \pm 0.62
	VR	13.0 \pm 12.4	16.7 \pm 18.2	21.6 \pm 16.3	62.6 \pm 35.0
	CS	4	10	13	13
20	SR	1.98 \pm 0.31	2.34 \pm 0.58	2.11 \pm 0.28	2.17 \pm 0.48
	VR	16.9 \pm 12.5	33.3 \pm 27.0	25.1 \pm 15.4	35.6 \pm 17.8
	CS	14	14	12	11
30	SR	1.77 \pm 0.18	1.76 \pm 0.25	1.72 \pm 0.20	1.90 \pm 0.36
	VR	19.6 \pm 15.4	23.3 \pm 18.6	20.8 \pm 18.4	26.4 \pm 17.4
	CS	13	10	12	10
40	SR	1.44 \pm 0.23	1.62 \pm 0.20	1.64 \pm 0.30	1.75 \pm 0.42
	VR	8.6 \pm 9.9	18.7 \pm 17.1	14.3 \pm 12.3	28.6 \pm 19.3
	CS	9	9	9	7

ments parallel to the drop-off, and those perpendicular to it, were compared (Student's t-test). In only one quadrat (II-20) out of 16 was there a significant difference ($t = 2.58$, $p < 0.05$) between these measures. This finding indicates that in most cases, a set of measurements in only one dimension should suffice to give a representative SR value.

In order to determine if there were significant changes in SR values down a transect, all pairs of quadrats along each transect were tested (Duncan's Multiple Range Test). At transect I, all pairs but one were significantly different from each other while the remaining three transects had fewer differences (Table 32). The four quadrats at the same depth were also compared with each other. The 10 m values were all significantly different from each other, while 20 and 40 m had only one significantly different pair and 30 m had none (Table 33).

The percentage substrate cover data for all of the quadrats (Table 34) may be represented as two triangular plots (Fig. 21). This technique depicts the proportions of the three principal categories of the substrate as a single point (see MacArthur et al. 1962). Several trends are apparent. The only quadrats with a large amount of sand are at 10 and 20 m. None of the Bonaire quadrats has any significant amount of sand. The glomerate category dominates at 30 and 40 m along all transects and most of it is composed of coral rock (Fig. 21). The coverage by ramose corals at all depths is relatively small. The quadrat with the largest ramose coverage (I-10) was essentially a monospecific stand of Madræcis mirabilis.

TABLE 32 - Comparison of the SR of all pairs of quadrats down each transect (Duncan's Multiple Range Test). A connecting line indicates means which are NOT significantly different ($p < 0.05$) from each other.

Depth (m)	Transects			
	I	II	III	IV
10	1.28	1.65	2.06	3.62
20	1.97	2.34	2.11	2.17
30	1.77	1.76	1.72	1.90
40	1.44	1.62	1.64	1.75

TABLE 33 - Comparison of the SR of all pairs of quadrats at the same depth (Duncan's Multiple Range Test). A connecting line indicates means which ARE significantly different ($p < 0.05$) from each other.

Depth (m)	Transects			
	I	II	III	IV
10	1.28	1.65	2.06	3.62
20	1.97	2.34	2.11	2.17
30	1.77	1.76	1.72	1.90
40	1.44	1.62	1.64	1.75

TABLE 34 - Percentage substrate cover by principal categories for 12 quadrats at Curaçao and 4 quadrats at Bonaire.

Quadrat	Glomerate corals		Ramoses corals		Sand
	Live	Dead	Live	Dead	
I-10	5.5%	3.4%	55.8%	30.6%	4.7%
-20	14.1	14.3	13.5	3.2	54.9
-30	15.1	64.5	2.2	0.0	18.2
-40	5.5	61.0	5.1	0.0	28.4
II-10	10.8	6.6	10.7	3.4	68.5
-20	16.4	65.9	6.8	2.3	8.6
-30	11.2	54.1	7.5	2.0	25.2
-40	3.8	59.4	13.4	1.8	21.6
III-10	23.5	14.6	0.7	3.1	58.1
-20	13.6	11.9	12.3	7.4	54.8
-30	4.1	68.3	21.8	2.3	3.5
-40	3.1	56.2	32.7	7.0	1.0
IV-10	11.8	7.4	48.2	28.5	4.1
-20	14.3	4.9	22.9	54.8	3.1
-30	15.4	49.8	29.3	2.5	3.0
-40	9.9	69.6	12.8	1.8	5.9

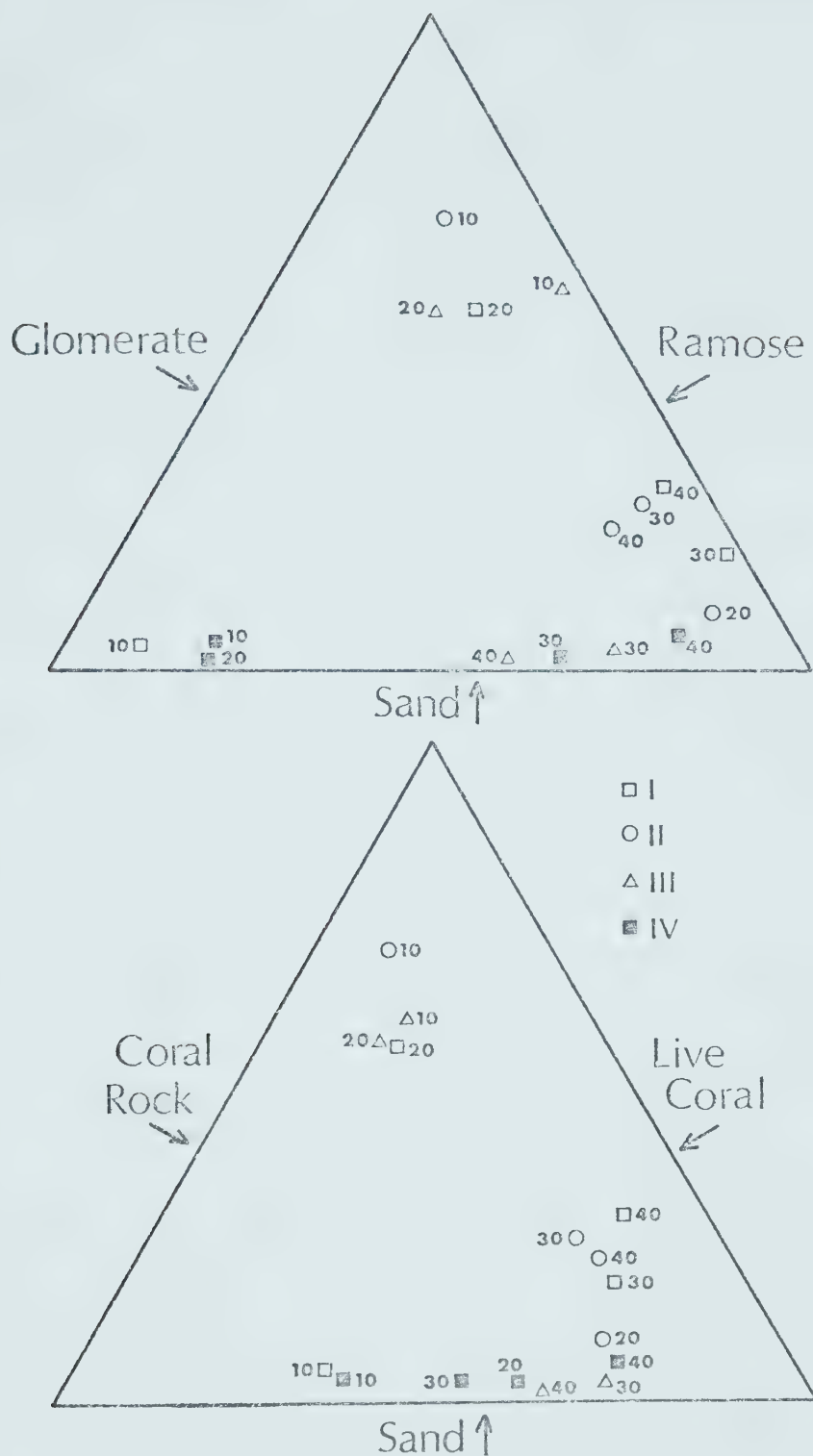


FIG. 21 - Triangle diagrams of percentage substrate cover by principal categories in quadrats along three transects (I, II, III) at Curaçao and one transect (IV) at Bonaire. Numbers are depths of quadrats.

Discussion

The range of individual SR values in this study probably represents a large proportion of the substrate rugosity conditions found on coral reef tracts in the Caribbean. Individual patch reefs would certainly yield higher values, as might single species stands (e.g. Acropora palmata), but such stands were not included in the present study. The conditions on most reefs range from flat, sandy areas to coral rubble to caves and overhangs. The highest individual SR value recorded was 4.60 in Bonaire (10 m) in a region where vertical relief was about 1.5 m. Risk (1972) obtained the equivalent of an SR of 4.0 as a maximum value in the shallow waters (4.5 m) around St. John, U.S. Virgin Islands.

The finding that the SR and VR were highly correlated, despite the large variation in topographic complexity on the reef, is significant. In areas with greater relief, it becomes increasingly difficult to make accurate SR measurements and the use of VR measures thus becomes easier and faster. Dahl (1973) has pointed out that the vertical relief of peaks and their frequency of occurrence are two important parameters necessary for the estimation of surface area.

The substrate rugosity patterns with depth show considerable variability, but one trend is apparent. The values at 10 m are the most variable, representing a wide range of substrate conditions. The values at 20 m are generally high and there is a consistent decrease to 40 m. The similarity in these patterns, from 20 to 40 m, is probably related to

the similar geomorphology of the reef slopes of the two islands. The physical factors influencing coral colony development and growth at each depth are also important. The lack of significant differences in SR in quadrats at the same depth (except 10 m) is probably best explained by a combination of these factors.

Coral species richness (CS) shows a consistent decrease with depth from 10 to 40 m (Table 31). Bak (1975) remarked on the high coral density and diversity on the reef slope of the SW coasts of Curaçao and Bonaire and the rapid decrease in these two parameters below 35-40m. This decrease is reflected in the lower CS values at the greater depths.

Correlation of fish parameters with substrate variables

The three substrate variables determined in the field (SR, VR, CS) were tested (correlation coefficient) against the fish community parameters. Three significant correlations were found at Curaçao, N_0 with SR and VR, and N with SR (Table 35). A similar analysis was made of the Bonaire data and many correlations were found to be significant (Table 35). These correlations are unusually high considering the small sample size ($N = 4$). At both islands, N_0 was highly correlated with SR, and N was also significantly correlated with SR. A scattergram of N_0 against SR for both islands was plotted (Fig. 22). Linear and curvilinear regressions were calculated for each island, and for the combined data, but the linear regressions provided the best fit. The regression line for each island was plotted (Fig. 22); the slopes of these lines were found not to be significantly different from each other ($t = 1.74$, NS).

In addition two other sets of substrate variables were tested. They were the variances (s^2) and coefficients of variation ($CV = 100 SD/\bar{X}$) of SR and VR. The rationale for using these two measures is that the variability of substrate topography may be as important in determining community parameters as the mean quantity of the same substrate variable. These measures were generally poorly correlated with the community parameters and only one significant positive correlation was found, that between CV (SR) and N_1 ($r = 0.595$, $p < 0.05$) in Curaçao. Finally, the transformed (arc sin) per-

TABLE 35 - Correlation matrix of substrate variables and fish community parameters from 12 quadrats at Curaçao (Cur.) and four quadrats at Bonaire (Bon.). All coefficients calculated with mean quadrat values except CS.

Substrate variables	Location	Fish Community Parameters				
		N ₀	N	NCP	N ₁	N ₂
SR	Cur.	0.782**	0.583*	0.361	0.537	0.280
	Bon.	0.992**	0.984*	0.981*	0.958*	0.919
VR	Cur.	0.690*	0.542	0.259	0.231	-0.010
	Bon.	0.985*	0.996**	0.985*	0.951*	0.923
CS	Cur.	0.551	0.463	0.172	0.469	0.333
	Bon.	0.888	0.821	0.722	0.676	0.578

* $p < 0.05$

** $p < 0.01$

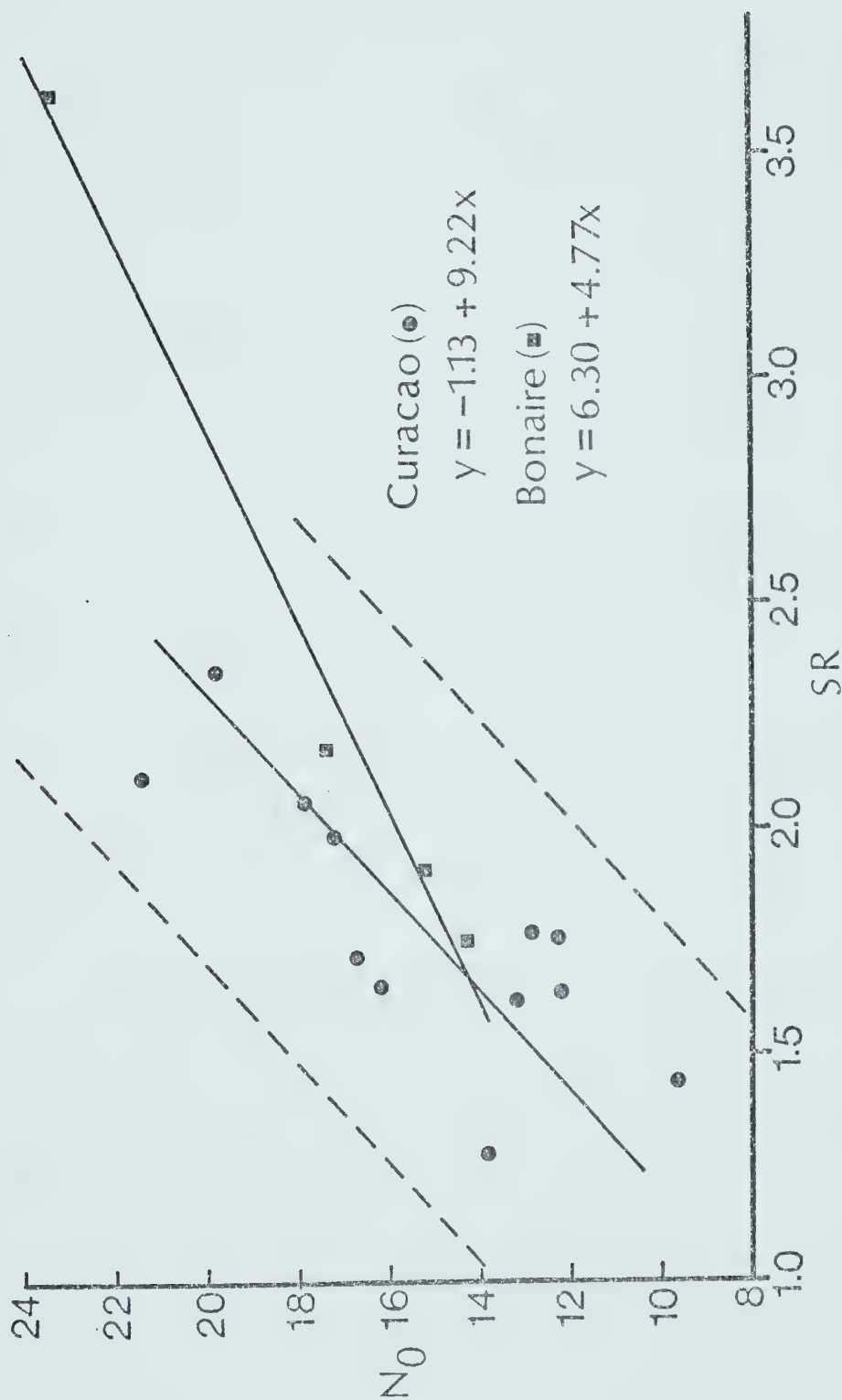


FIG. 22 - Linear regressions of substrate rugosity (SR) against resident species richness (N_0) for Curaçao and Bonaire. The 95% confidence limits for the Curaçao regression line are indicated.

centage cover data were tested against the community parameters. Two significant correlations were found, both negative, and neither was readily ecologically interpretable.

The three initial substrate variables (SR, VR, CS) were then used in a stepwise multiple regression analysis with each of the community parameters. In all cases, SR accounted for the greatest proportion of variation in the dependent variable. The contribution of VR and CS varied with different parameters, but was generally small. However, because SR was highly intercorrelated with VR ($r = 0.848$, $p < 0.001$), and more surprisingly CS ($r = 0.856$, $p < 0.001$), this set of variables was considered unsuitable for multiple regression interpretation as the results become less reliable with high multicollinearity (Nie et al. 1975). For the same reason, the variances and coefficients of variation of SR and VR could not be used in a multiple regression. As a consequence, SR was used alone in a simple regression analysis.

Further evidence for the assertion that SR was the most important substrate variable comes from the partial correlation coefficients calculated from the same data set. N_0 was still significantly correlated with SR when VR and CS were held constant (Table 36), but it showed no correlation with VR as it had in the simple correlation coefficient analysis (Table 35). The most likely interpretation of this finding is that VR is an essential component of SR, i.e. vertical relief enhances rugosity, but the converse is not necessarily true. It is possible to have a large VR but a

TABLE 36 - Partial correlation coefficient matrix of substrate variables and fish community parameters from 12 quadrats at Curaçao. Each coefficient is calculated holding the remaining two substrate variables constant.

Substrate variables	Fish community parameters				
	N_0	N	NCP	N_1	N_2
SR	0.576*	0.203	0.444	0.592*	0.373
VR	-0.087	0.082	-0.250	-0.541	-0.458
CS	-0.370	-0.044	-0.362	-0.239	-0.021

* $p < 0.05$

relatively small SR, e.g. a large glomerate coral head.

The only other significant partial correlation was that between N_1 and SR, indicating that SR may have some influence on diversity. All coefficients with VR and CS were either close to zero or negative. The relatively high negative partial correlations between VR and N_1 and N_2 (Table 36) are of some interest. They serve to confirm that SR is the most important variable influencing diversity because when SR is held constant, and VR is increased, rugosity is effectively decreased. A decrease in diversity occurs under these conditions.

The relationship between N_0 and SR, once established, provided the opportunity to use it in a predictive capacity. An attempt was made to predict N_0 from the mean SR of two experimental quadrats. These two quadrats were randomly chosen in the general areas of the other transects in Curaçao, one at 10 m and the other at 20 m. The SR measurements were made and the mean value calculated. The value of N_0 for each experimental quadrat was then predicted from the regression line (Fig. 22). Several censuses were conducted in each quadrat over a two week period to obtain estimates of N_0 . The value for the 10 m quadrat was in close agreement with that predicted, but the 20 m value was less accurate (Table 37). However, both predicted values fell within the 95% confidence limits of the regression line (Fig. 22).

The relationship between selected species and specific substrate variables was also investigated. The species chosen were those which had marked substrate preferences. Three common gobiid species found at all depths, were considered to be suit-

TABLE 37 - Comparison of observed values of resident species richness (N_0) from two experimental quadrats with those predicted from a linear regression.

Quadrat depth (m)	SR	Observed N_0	Predicted N_0	Residual ($Y' - Y$)
10	1.89	15	16.3	1.3
20	1.88	20	16.2	3.8

able test species. During extensive field observations they were rarely observed away from their preferred substrate. Two of these species, Coryphopterus glaucofraenum and Gnatholepis thompsoni, were invariably associated with sand and the third species, Coryphopterus lipernes was found on live, usually glomerate coral heads. Correlations were sought between the mean number (N) of each of these species (over a 14 month period) and the area of their preferred substrate in the quadrats at Curaçao. The transformed (arc sin) area values were used in the calculations. The mean values of N were calculated excluding the recruit size category. This was done because of the greater inaccuracy of the recruit counts due to the difficulty in detecting them on the sand, and to the large, short-term fluctuations in abundance which affect the means.

Both species associated with sand yielded significant correlations (C. glaucofraenum, $r=0.821$, $p<0.01$; G. thompsoni, $r=0.620$, $p<0.05$). The numbers of C. lipernes showed no significant correlation with either the area of glomerate coral (live) ($r=0.416$, NS) or total coral (live) ($r=0.332$, NS).

Discussion

Coral reefs are topographically complex. The substrate is biologically generated and the corals are subject to numerous factors which affect growth, form and distribution. The quantification of such a complex substrate is necessarily a rough approximation and most measures yield only gross estimates. The scale at which the investigator is working is an important consideration when determining the degree of precision required. Dahl(1973) has developed techniques for estimating the surface

area along reef transects by using geometrical approximations of known area and fitting them to common biological substrates on the reef. He divided his theoretical reef surfaces into three scales: 1. gross reef morphology, 2. individual corals and 3. coral or rock surfaces. This was necessary as he was concerned with the substratum available for benthic macro-algae. The scale most significant to reef fishes for shelter is scale 1 and this is the level at which measures have usually been made. Scale 2 is important for many of the smaller species e.g. clinids and gobies, but little work has been done at this level. Talbot and Goldman (1972) used two different techniques to quantify habitat complexity - numbers of holes of three different size categories and an estimate of bottom surface area using a piece of line. Risk (1972) measured habitat complexity on the reef by using a series of chain measurements as estimates of surface area. In the present study, a similar technique using chain measurements was employed to obtain an estimate of surface rugosity (SR). In addition, vertical relief (which is important in producing habitat patchiness) was also measured. The SR, although a function of substrate complexity, is not a measure of heterogeneity as it is normally characterized. It is essentially an estimate of surface area, and as such is not strictly comparable with other measures of habitat heterogeneity.

Several studies on coral reef fishes have noted the presumed effect of the complexity of the reef and the resulting increase in surface area, on fish populations (Bardach 1959; Randall 1963). Hiatt and Strasburg (1960) found more

species and individuals on "ramose" coral heads than on "glomerate" heads. They suggested that this was probably due to the lack of hiding places on the glomerate heads. Talbot (1965) indicated that there was a "clear relationship between quantity and complexity of fish population species structure with percentage and type of cover of the bottom". In one of the few quantified studies on the reef, Risk (1972) tested all of his substrate variables with two fish community parameters (diversity and total numbers). He found only one significant correlation, that between diversity and substrate topographic complexity. The number of fishes was not significantly correlated with complexity or with the biological diversity of the substrate. Talbot and Goldman (1972) determined that fish species richness did not correlate well with either number of holes or surface area, but it did fit well in a combined index which included two physical variables viz. wave action and temperature variation. However, the variables were used only in a ranking procedure thus making it difficult to assess the significance of this correlation.

Such studies suggest that substrate complexity is an important factor determining fish species richness and diversity. It appears that increased complexity (surface area) is providing a greater diversity of shelter sites, thus enhancing species richness. This relationship may not be valid for a single species coral stand because of the limited diversity of shelter sites (Talbot 1965). The increase in complexity reflects not only the potential shelter sites available for

fishes and their prey, but also the surface area available for occupation by algae and invertebrates. The number of fishes was probably not highly correlated with the SR because the fish species utilize several space-sharing mechanisms. This obscures a simple relationship between number of shelter sites and number of individuals. Neither measure of diversity was significantly correlated with the substrate variables in Curaçao, although the partial correlation between N_1 and SR was significant (0.05 level). This indicates that rugosity is of some importance in its effect on the diversity of the fishes using a given substrate.

None of the measures of substrate coverage showed any significant positive correlations with the community parameters, but several were found with individual species. A highly significant area effect was determined for the sand-dwelling goby, Coryphopterus glaucofraenum. This suggests that fish (mature and juvenile) occupy home ranges within a certain size range and that the number of individuals present is generally governed by the area of sand available. Several brief observation periods showed that mature individuals moved within a circumscribed area (usually 50 cm diameter). Smith and Tyler (1972) list the home range of this species in their study simply as a "ring", but give no dimensions. The mean number of Gnatholepis thompsoni was also correlated with area. This species is often found with C. glaucofraenum but it appears to prefer sandy areas with more rubble. The numbers of C. lipernes were not correlated with either the area

of live glomerate corals or total live corals. Other factors, in addition to substrate, are obviously important in determining density and distribution in this species.

SUMMARY AND CONCLUSIONS

The resident fish communities along depth transects on the fringing reefs of Curaçao and Bonaire were basically similar in various aspects of community structure - trophic composition, activity periods and home range designations. The three Curaçao transects were very similar to each other in all aspects indicating little variation in the communities at different locations. Some differences were found with the single Bonaire transect but I do not believe that they indicate significant differences in community organization.

The planktivores formed the largest percentage of the community in all quadrats. This predominance is not surprising as most of the resident species had small home ranges and plankton is a food source which may be obtained without having to move over the reef to forage. The importance of reef plankton to many of the small resident species has probably been underestimated in the past. Species living within the reef infrastructure e.g. Liopropoma rubre have also been observed taking reef plankton near a cave entrance. The number of large carnivorous species (mainly groupers) is higher at Bonaire than at Curaçao probably owing to the decreased spearfishing pressure (the reefs are part of a marine park). The long term effect on reef fish community structure of a change in the predator populations at Bonaire would provide valuable insight into the influence of predators on the communities.

Most of the resident fishes were diurnally active; the nocturnal element of the communities generally comprised less

than 25%. Those species designated as cryptic, either by colouration e.g. Enneanectes atlorus or microhabitat preference e.g. Liopropoma mowbrayi, made up a substantial proportion of the community in most quadrats. The ecology and behaviour of the species forming this segment of the community is very poorly known. I have paid particular attention to a number of these species during extensive observations and have determined some aspects of their ecology, viz. feeding and space utilization. Further study is necessary to clearly define their role in the community.

The nocturnal communities were characterized by non-resident planktivores seeking shelter in the reef and apogonids foraging above the substrate. At night, the nocturnal species vacate their shelter sites to feed over the reef. The resident diurnal species settle into their nocturnal resting places and the non-residents "pack" into the remaining space available. I have evidence that at least one non-resident species, Clepticus parrai, consistently uses the same sites at night. The markedly higher nocturnal abundance of apogonids indicates that many individuals are sequestered in the reef during the day where they cannot be detected. Since many apogonid species feed together within a small area, it appears that competition for the same food source is reduced by feeding at different heights above the substrate.

The communities along the transects were compared by two indices, the coefficient of community and Euclidean distance. At Curaçao, there was a major change in species composition

in passing from the 10 m quadrat, on the edge of the reef platform, over the drop-off, to the 20 m quadrats on the reef slope. The deeper communities (30 and 40 m) showed high similarity with the CC index but were more variable when the relative abundance of the species was considered (D index). The single Bonaire transect had a similar CC pattern but the D values indicated greater uniformity in composition with depth. Several more transects would need to be investigated to determine the consistency of the pattern at Bonaire.

The distribution of the species which comprise the communities is influenced by many factors, including competition, predation and food availability. Apparent depth preferences of species may be influenced by any, or all, of these factors in addition to substrate preference. Differences in the depth ranges of a few species between Curaçao and Bonaire were noted. These were attributed largely to substrate differences, but other factors may also have been involved. Although there is usually specificity in the broad type of habitat occupied, many species are probably not microhabitat specialists. Several species (e.g. Amblycirrhitus pinos, Acanthemblemaria spinosa) were found only in the 10 m quadrats while others (e.g. Liopropoma mowbrayi, Chronis scotti) were recorded only at 30m and 40m. About 15 resident species occurred at all depths and perhaps 10 of these were found in every quadrat. Most of these species were gobiids, some of which had definite substrate preferences (e.g. sand, live coral), while others apparently did not. The reasons for these differences in distribution are the

result of a complex of interacting factors. The elucidation of these factors will require a more thorough knowledge of the way in which reef fish communities are structured and maintained. A useful starting point for species distribution would be a gradient analysis such as the one conducted by Terborgh (1971) on birds in the Andes. His three theoretical models of species distribution might profitably be tested on reef fishes.

The diversity patterns along the transects were analyzed using Hill's diversity numbers. In Curaçao, N_0 increased from 10 m to 20 m and then declined to 40 m. In Bonaire, there was a steady decline from 10 to 40 m. The two diversity measures, N_1 and N_2 , exhibited no consistent trends. The beta diversity of the transects appears to be high, values ranging from 0.57 to 1.00. In the latter case, there is a complete species turnover in a 30 m depth range. The lowest value (from Bonaire) indicates greater homogeneity in species composition than at Curaçao.

The patterns of diversity along the depth gradients are the result of both biological and physical factors. Several substrate variables were tested against the diversity numbers. A significant correlation was obtained between resident species richness and a measure of the substrate rugosity in the quadrat. The importance of the topographic complexity of the reef in enhancing the number of species residing there has long been recognized. The finding of this study further supports this contention. In addition, the relationship was tested in two experimental quadrats and the results were found to be in agree-

ment with those predicted.

The recruitment patterns of 16 resident species were examined by counting the number of size-designated postlarval recruits in all quadrats. The overall pattern of occurrence and abundance for the combined Curaçao transects showed that most of the species had two peaks of abundance, one in the spring and one in the autumn. Comparisons with the limited Bonaire recruitment data were made in several species. Generally the patterns were similar in corresponding months. Members of the Gobiidae appeared to have more than two peaks. The species with the largest sample sizes had recruits present throughout the year, indicating the existence of a surplus pool of fishes capable of colonizing any vacated area.

A temporal analysis of four community parameters was made to detect evidence of changes in community structure and possible seasonal trends during the 18 month study period. Species richness was mainly linear with some fluctuations. In most quadrats, there was an initial rapid increase in N_0 as more species, particularly cryptic ones, were detected by repeated visual sampling.

The number of fishes (NCP) exhibited large fluctuations in abundance (two or three fold) which appeared to be seasonal. This finding is in contrast to an earlier supposition (Smith and Tyler 1972) that there was no evidence of large fluctuations in abundance of reef fishes throughout an annual cycle. However, these authors did not have the benefit of continuous census data at a site over a period of a year. NCP was highly correlated with water temperature suggesting the influence of

reproductive periodicity on changes in abundance. The individual recruitment patterns of the species in the communities provide a possible explanation. The additive effect of peaks in recruit abundance in different species at the same time of the year (autumn) would be sufficient to produce a marked increase in NCP. A subsequent decrease in the recruitment rate, allowing predators to remove more recruits than were being added, would cause NCP to decrease. Any factors affecting the recruitment patterns could also markedly affect the pattern of NCP. A number of annual cycles would be required to determine if this seasonal pattern in NCP is consistent.

The temporal variation in both diversity (N_1) and evenness ($E_{2.1}$) showed no consistent trends during the study. Overall, there was little evidence of seasonal changes in these two parameters.

Chance events of mortality (mainly by predation) and recruitment probably play a central role in determining the long term species composition and diversity of a small reef area. There will be a continual influx of postlarval fishes in varying abundance throughout the year. Some may settle in recently vacated areas and be successful in establishing there. Others may be excluded by larger, mature fish or by the competitively superior postlarvae of other species. Many will be eaten by predators, particularly if they settle in an unsuitable habitat. At any rate, there are bound to be large differences in survivorship in different habitats. Recruitment will thus replenish the losses to populations as well as pro-

viding colonizing members of new species.

The patterns of space utilization of community members will further influence community structure. Different species have evolved different strategies for obtaining and holding space. Some show site specificity whereas others are generalists. Juvenile and adult fishes frequently occupy different habitats. All of these factors produce a mosaic of differing space utilization. The territorial pomacentrids, by virtue of their constant occupation of an area, have a strong influence on the use of space by the more labile species. Within the reef infrastructure, the holocentrids show the highest degree of spatial constancy followed by the apogonids. The species residing in tube-worm holes and sponges frequently show high spatial constancy as well. The findings of this study generally confirm that space is intensively used on reefs and that spatial constancy in a number of species is very high.

It is becoming clear that the patterns of diversity and species composition in reef fish communities will not be explained by one general mechanism, but by many mechanisms acting simultaneously at different levels. The elucidation of these mechanisms will require a great deal of experimental field work and hypothesis testing to augment the basic descriptive data now available.

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APPENDIX A

APPENDIX A1 - Space utilization by resident species in quadrat I-10. The values given are mean \pm SD (range). For complete species names and explanation of site code, see Table 25.

Site code	Species	No. of sites	Constancy (%)	Consistency (%)	Time span (weeks)
2. <u>A. pinos</u>		4	44.8 \pm 29.4 (25-88)	43.5 \pm 23.2 (28-78)	31.8 \pm 23.3 (15-65)
<u>C. arai</u>		1	75.0	67.0	76
3. <u>A. townsendi</u>		1	72.0	85.0	57
<u>E. nipoliti</u>		5	27.0 \pm 7.6 (19-38)	36.8 \pm 15.6 (19-56)	17.2 \pm 4.8 (12-24)
5. <u>A. spinosa</u>		1	16.0	14.0	8
<u>E. bahamensis</u>		2	30.0 \pm 24.0 (13-47)	36.5 \pm 30.4 (16-58)	11.7 \pm 5.1 (6-29)
6. <u>S. hassi</u>		1	25.0	80.0	23

APPENDIX A2 - Space utilization by resident species in quadrat I-20. The values given are mean \pm SD (range). For complete species names and explanation of site code, see Table 25.

Site code	Species	No. of sites	Constancy (%)	Consistency (%)	Time span (weeks)
1. <u>E. planifrons</u>		4	78.0 \pm 25.4 (56-100)	98.8 \pm 2.5 (95-100)	60.5 \pm 23.7 (39-81)
2. <u>E. atrovus</u>		1	16.0	24.0	10
3. <u>E. loreto</u>		1	13.0	25.0	6
4. <u>H. hinoliti</u>		19	34.0 \pm 14.3 (19- 63)	53.8 \pm 22.7 (21- 94)	21.7 \pm 9.2 (8-40)
4. <u>H. marianus</u>		3	48.0 \pm 45.1 (19-100)	56.0 \pm 35.4 (24- 94)	38.7 \pm 22.6 (16-76)
1. <u>L. rubro</u>		3	22.0 \pm 10.8 (13- 34)	46.0 \pm 15.0 (31- 61)	22.7 \pm 15.6 (8-39)
1. <u>L. trilineata</u>		3	20.0 \pm 6.9 (16- 28)	31.7 \pm 18.5 (21- 53)	16.3 \pm 11.0 (10-29)
P. <u>retrospinis</u>		2	33.0 \pm 11.3 (25- 41)	43.5 \pm 9.2 (37- 50)	39.5 \pm 6.4 (35-44)

APPENDIX A3 - Space utilization by resident species in quadrat I-30. The values given are mean \pm SD (range). For complete species names and explanation of site code, see Table 25.

Site code	Species	No. of sites	Constancy (%)	Consistency (%)	Time span (weeks)
1. <u>E. partitus</u>		2	92.5 \pm 6.4 (88-97)	88.5 \pm 7.8 (83- 94)	72.0 \pm 5.7 (68-76)
3. <u>G. loreto</u>		6	36.5 \pm 19.2 (16-69)	53.7 \pm 27.4 (28-100)	23.3 \pm 14.4 (8-48)
2. <u>hipoliti</u>		16	34.9 \pm 11.8 (13-53)	54.5 \pm 18.1 (24- 81)	22.1 \pm 7.7 (8-34)
4. <u>A. rhodan</u>		2	33.0 \pm 19.8 (19-47)	49.0 \pm 4.2 (46- 52)	30.0 \pm 22.6 (14-46)
<u>L. carnabi</u>		1	13.0	16.0	24
<u>L. trilineata</u>		2	25.0 \pm 4.2 (22-28)	35.0	24.5 \pm 14.9 (14-35)

APPENDIX A4 - Space utilization by resident species in quadrat I-40. The values given are mean \pm SD (range). For complete species names and explanation of site code, see Table 25.

Site code	Species	No. of sites	Constancy (%)	Consistency (%)	Time span (weeks)
3, <u>G.</u>	<u>lorato</u>	3	42.7 \pm 13.1 (23-53)	47.3 \pm 5.5 (42-53)	32.7 \pm 7.5 (24-37)
<u>G.</u>	<u>hinoliti</u>	9	23.3 \pm 7.4 (13-34)	37.2 \pm 11.6 (18-50)	14.9 \pm 4.9 (8-22)
4, <u>A.</u>	<u>phenax</u>	1	25.0	44.0	36
<u>L.</u>	<u>mombravi</u>	1	19.0	33.0	22
<u>P.</u>	<u>retrospinis</u>	1	13.0	80.0	13

APPENDIX A5 - Space utilization by resident species in quadrat II-10. The values given are mean \pm SD (range). For complete species names and explanation of site code, see Table 25.

Site code	Species	No. of sites	Constancy (%)	Consistency (%)	Time span (weeks)
1. E.	<u>diencaeus</u>	3	83.3 \pm 28.9 (50-100)	100.0	65.0 \pm 26.0 (35-80)
E.	<u>planiifrons</u>	1	69.0	61.0	50
2. A.	<u>pinos</u>	6	53.2 \pm 25.7 (22- 88)	58.0 \pm 17.5 (34- 78)	47.5 \pm 16.7 (24-68)
3. C.	<u>hiroliti</u>	8	24.5 \pm 15.6 (13- 56)	32.6 \pm 18.7 (19- 75)	15.5 \pm 10.1 (2-36)
5. A.	<u>spinosa</u>	15	33.9 \pm 23.5 (13-100)	49.8 \pm 33.8 (15-100)	21.1 \pm 16.3 (6-67)
E.	<u>bahamensis</u>	4	17.5 \pm 3.9 (13- 22)	34.3 \pm 20.5 (15- 60)	11.3 \pm 4.5 (6-15)
6. C.	<u>horsti</u>	1	100.0	100.0	76

APPENDIX A6 - Space utilization by resident species in quadrat II-20. The values given are mean \pm SD (range). For complete species names and explanation of site code, see Table 25.

Site code	Species	No. of sites	Constancy (%)	Consistency (%)	Time span (weeks)
1. <u>E. partitus</u>		4	75.8 \pm 28.7 (44-100)	93.3 \pm 10.4 (78-100)	58.0 \pm 23.5 (33-80)
<u>E. planifrons</u>		2	53.0 \pm 59.4 (16-100)	85.5 \pm 20.5 (71-100)	43.5 \pm 38.9 (16-71)
2. <u>E. atropus</u>		3	39.7 \pm 18.6 (22- 59)	43.7 \pm 16.6 (26- 59)	42.7 \pm 28.0 (12-67)
3. <u>G. loreto</u>		10	47.4 \pm 12.8 (28- 63)	79.0 \pm 17.9 (41- 95)	37.3 \pm 8.3 (25-47)
<u>G. hinoliti</u>		13	28.8 \pm 13.7 (13- 53)	45.2 \pm 21.1 (18- 94)	18.3 \pm 8.8 (8-34)
4. <u>A. rhodex</u>		4	31.5 \pm 20.0 (13- 53)	50.8 \pm 12.8 (36- 67)	28.5 \pm 22.5 (10-58)
<u>H. marianus</u>		2	76.5 \pm 33.2 (53-100)	70.5 \pm 26.2 (52- 80)	64.5 \pm 16.3 (53-76)
<u>L. rubra</u>		8	35.0 \pm 20.1 (13- 72)	49.4 \pm 27.6 (17-100)	33.5 \pm 18.2 (8-49)
<u>L. trilineata</u>		4	40.8 \pm 29.4 (13- 78)	49.3 \pm 20.0 (26- 74)	39.5 \pm 26.1 (14-68)
<u>P. retrocinis</u>		2	50.0 \pm 48.1 (16- 84)	54.0 \pm 29.7 (33- 75)	51.5 \pm 34.7 (27-76)
5. <u>E. bahamensis</u>		1	13.0	100.0	8

APPENDIX A7 - Space utilization by resident species in quadrat II-30. The values given are mean \pm SD (range). For complete species names and explanation of site code, see Table 25.

Site code	Species	No. of sites	Constancy (%)	Consistency (%)	Time span (weeks)
1. <u>E. partitus</u>		3	65.3 \pm 11.0 (59-78)	58.3 \pm 9.2 (53- 69)	49.3 \pm 0.6 (49-50)
3. <u>E. loreto</u>		15	34.3 \pm 18.2 (13-69)	53.3 \pm 28.9 (18-100)	22.4 \pm 14.3 (6-47)
2. <u>hipoliti</u>		20	37.5 \pm 24.1 (16-94)	48.4 \pm 22.6 (24- 94)	23.9 \pm 15.4 (10-60)
4. <u>A. phenax</u>		4	19.8 \pm 7.9 (13-31)	45.0 \pm 36.9 (21-100)	15.0 \pm 10.1 (8-30)
<u>L. rubre</u>		4	39.3 \pm 23.7 (19-72)	36.5 \pm 19.6 (21- 64)	37.5 \pm 27.8 (12-68)
<u>L. trilineata</u>		3	15.0 \pm 3.5 (13-19)	20.0 \pm 6.3 (13- 25)	11.7 \pm 3.5 (8-15)

APPENDIX A8 - Space utilization by resident species in quadrat II-40. The values given are mean \pm SD (range). For complete species names and explanation of site code, see Table 25.

Site code	Species	No. of sites	Constancy (%)	Consistency (%)	Time span (weeks)
3. A.	<u>townsendi</u>	1	22.0	27.0	14
G.	<u>loreto</u>	15	38.3 \pm 23.8 (16-100)	53.7 \pm 26.0 (21-100)	32.4 \pm 20.1 (6-76)
Q.	<u>hiboliti</u>	16	34.9 \pm 18.9 (13- 72)	48.3 \pm 22.7 (16- 96)	22.3 \pm 12.2 (8-46)
4. H.	<u>marianus</u>	1	31.0	28.0	61
L.	<u>moreira</u>	1	13.0	25.0	13
L.	<u>trilineata</u>	1	13.0	24.0	12
P.	<u>retrospinis</u>	1	100.0	97.0	71

APPENDIX A9 - Space utilization by resident species in quadrat III-10. The values given are mean \pm SD (range). For complete species names and explanation of site code, see Table 25.

Site code	Species	No. of sites	Constancy (%)	Consistency (%)	Time span (weeks)
1. <u>E. planifrons</u>		4	84.5 \pm 31.0 (38-100)	93.8 \pm 12.5 (75-100)	65.3 \pm 21.5 (33-76)
2. <u>A. pinos</u>		5	46.2 \pm 27.0 (16- 84)	59.0 \pm 31.7 (19-100)	45.2 \pm 25.8 (10-69)
3. <u>M. jacobus</u>		2	61.0 \pm 50.9 (25- 97)	59.0 \pm 38.2 (32- 86)	64.5 \pm 16.3 (53-76)
4. <u>Q. hipoliti</u>		9	28.1 \pm 10.2 (16- 50)	45.7 \pm 13.5 (31- 76)	18.0 \pm 6.6 (10-32)
4. <u>E. punctatus</u>		1	41.0	42.0	46
H. <u>marianus</u>		1	72.0	64.0	76
5. <u>A. spinosa</u>		33	55.0 \pm 29.9 (13-100)	72.9 \pm 31.4 (13-100)	36.2 \pm 21.3 (6-69)
<u>E. bahamensis</u>		3	29.3 \pm 21.0 (13- 53)	33.7 \pm 27.3 (15- 65)	20.3 \pm 18.9 (7-42)
6. <u>G. horsti</u>		1	19.0	21.0	52
<u>S. hassi</u>		1	38.0	43.0	59

APPENDIX A10 - Space utilization by resident species in quadrat III-20. The values given are mean \pm SD (range). For complete species names and explanation of site code, see Table 25.

Site code	Species	No. of sites	Constancy (%)	Consistency (%)	Time span (weeks)
1. <u>E. planifrons</u>		2	100.0	100.0	76
2. <u>E. atrorus</u>		1	25.0	33.0	45
<u>M. ensenadae</u>		1	28.0	53.0	32
3. <u>A. townsendi</u>		8	35.5 \pm 18.0 (13-66)	53.3 \pm 23.6 (17- 88)	34.5 \pm 17.4 (8-51)
<u>G. loreto</u>		4	47.0 \pm 24.2 (19-78)	52.0 \pm 26.4 (27- 89)	33.0 \pm 18.9 (14-59)
<u>M. jacobus</u>		1	47.0	100.0	33
<u>P. cruentatus</u>		1	13.0	57.0	10
<u>G. hipoliti</u>		18	36.3 \pm 16.8 (16-72)	56.7 \pm 23.4 (26-100)	23.2 \pm 10.8 (10-46)
4. <u>A. lachneri</u>		4	35.0 \pm 16.4 (22-59)	43.8 \pm 19.7 (26- 67)	30.5 \pm 10.2 (16-39)
<u>A. phenax</u>		2	19.0 \pm 4.2 (16-22)	33.5 \pm 7.8 (28- 39)	32
<u>H. marianus</u>		3	32.3 \pm 23.3 (16-59)	36.3 \pm 17.0 (19- 53)	50.7 \pm 22.0 (36-76)
<u>L. rubre</u>		5	22.2 \pm 10.8 (13-38)	37.6 \pm 18.8 (17- 60)	22.0 \pm 14.3 (8-41)
<u>L. trilineata</u>		4	25.3 \pm 17.4 (13-50)	32.3 \pm 11.6 (21- 48)	21.3 \pm 21.5 (8-53)
<u>P. retrospinis</u>		2	72.0 \pm 4.2 (69-75)	71.0 \pm 2.8 (69- 73)	66.5 \pm 2.1 (65-71)
5. <u>E. bahamensis</u>		2	20.5 \pm 6.4 (16-25)	64.5 \pm 50.2 (29-100)	12

APPENDIX A11 - Space utilization by resident species in quadrat III-30. The values given are mean \pm SD (range). For complete species names and explanation of site code, see Table 25.

Site code	Species	No. of sites	Constancy (%)	Consistency (%)	Time span (weeks)
1. <u>E. partitus</u>		2	42.0 \pm 19.8 (28-56)	47.5 \pm 3.5 (45- 50)	34.5 \pm 17.7 (22-47)
2. <u>E. atrorubus</u>		1	22.0	47.0	31
3. <u>G. loreto</u>		21	26.4 \pm 14.9 (13-69)	48.1 \pm 26.9 (18-100)	19.1 \pm 12.0 (6-47)
<u>P. cruentatus</u>		1	50.0	44.0	76
<u>Q. hipolititi</u>		11	23.5 \pm 8.3 (13-38)	35.3 \pm 14.5 (17- 67)	14.9 \pm 5.4 (8-24)
4. <u>A. phenax</u>		4	22.3 \pm 14.6 (13-44)	31.3 \pm 7.9 (22- 41)	32.5 \pm 25.9 (8-69)
<u>H. marianus</u>		1	66.0	60.0	73
<u>L. carmabi</u>		1	13.0	25.0	20
<u>L. rubre</u>		8	20.5 \pm 6.6 (13-34)	39.3 \pm 18.4 (17- 79)	15.6 \pm 8.5 (8-30)
<u>L. trilineata</u>		6	25.8 \pm 18.5 (16-63)	36.3 \pm 20.9 (20- 77)	21.5 \pm 17.4 (10-56)
<u>P. retrospinis</u>		1	78.0	83.0	63

APPENDIX A12 - Space utilization by resident species in quadrat III-40. The values given are mean \pm SD (range). For complete species names and explanation of site code, see Table 25.

Site code	Species	No. of sites	Constancy (%)	Consistency (%)	Time span (weeks)
3. G.	<u>loreto</u>	5	24.6 \pm 9.8 (16-41)	31.4 \pm 9.4 (16-41)	18.0 \pm 11.7 (10-38)
	<u>P. cruentatus</u>	1	16.0	56.0	20
2.	<u>hipolititi</u>	3	33.3 \pm 17.0 (16-50)	38.3 \pm 13.1 (26-52)	21.3 \pm 11.0 (10-32)
4. A.	<u>phenax</u>	1	31.0	31.0	28
	<u>H. marianus</u>	2	61.0 \pm 28.3 (41-81)	58.5 \pm 31.8 (36-81)	46.0 \pm 29.7 (25-67)
	<u>E. rubre</u>	2	47.0 \pm 8.5 (41-53)	43.5 \pm 7.8 (38-49)	56.0 \pm 14.1 (46-66)
	<u>L. trilineata</u>	1	13.0	33.0	7
	<u>P. retrospinis</u>	1	31.0	63.0	28

APPENDIX B



APPENDIX B1 - Quadrat I-10 at Curaçao



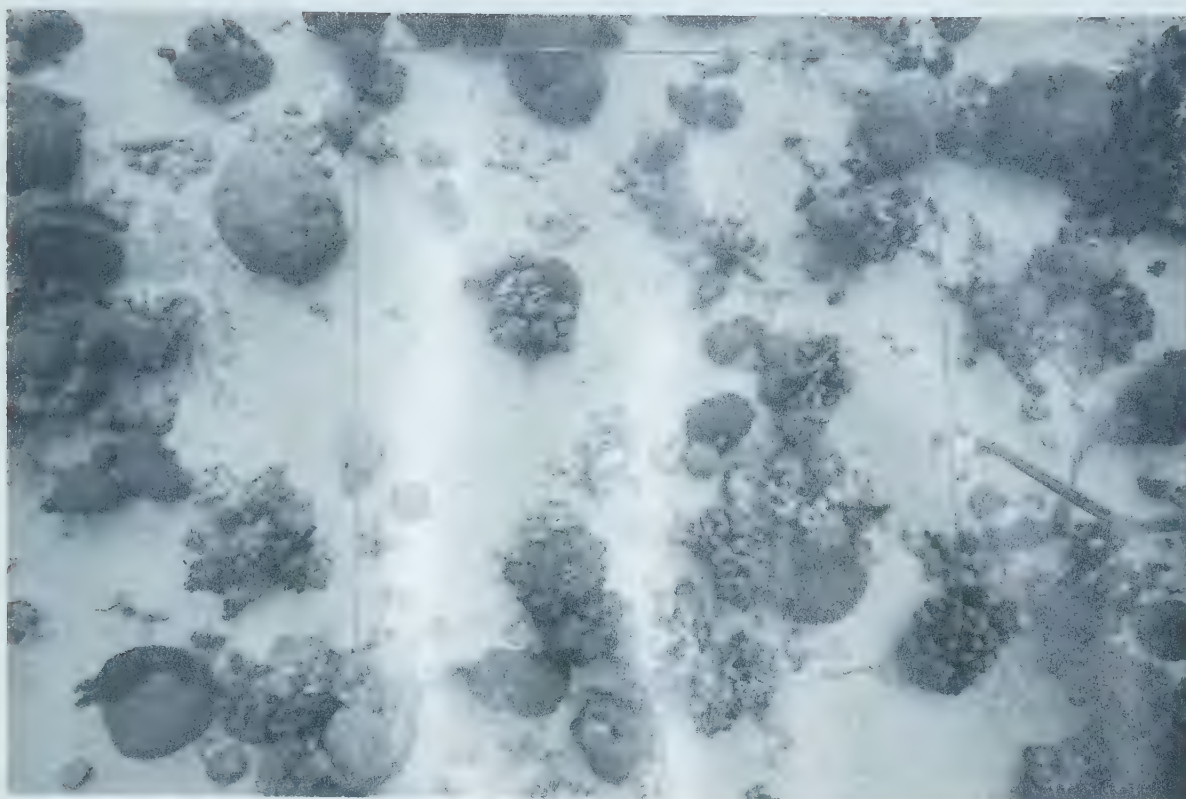
APPENDIX B2 - Quadrat I-20 at Curaçao



APPENDIX B3 - Quadrat I-30 at Curaçao



APPENDIX B4 - Quadrat I-40 at Curaçao



APPENDIX B5 - Quadrat II-10 at Curaçao



APPENDIX B6 - Quadrat II-20 at Curaçao



APPENDIX B7 - Quadrat II-30 at Curaçao



APPENDIX B8 - Quadrat II-40 at Curaçao



APPENDIX B9 - Quadrat III-10 at Curaçao



APPENDIX B10 - Quadrat III-20 at Curaçao



APPENDIX B11 - Quadrat III-30 at Curaçao



APPENDIX B12 - Quadrat III-40 at Curaçao





APPENDIX B14 - Quadrat IV-20 at Bonaire



APPENDIX B13 - Quadrat IV-10 at Bonaire





APPENDIX B16 - Quadrat IV-40 at Bonaire



APPENDIX B15 - Quadrat IV-30 at Bonaire

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